Aboveground Primary Productivity in Forest Ecosystems as a Function of Species Diversity and Composition

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

von

Nadia Cristina Castro Izaguirre

aus

Peru

Promotionskomitee:

Prof. Dr. Bernhard Schmid (Vorsitz)

PD Dr. Pascal A. Niklaus (Leitung der Dissertation)

Prof. Dr. Keping Ma

Prof. Dr. Andy Hector

Zürich, 2016

Abstract

In the last two decades, several studies have demonstrated that species richness enhances primary productivity. However, much uncertainty still exists about the relationship between biodiversity and ecosystem functioning (BEF) in forests, especially in highly diverse biomes. This is a primary concern for human welfare as forests play a major role in carbon sequestration at global scale and in providing numerous services. On the other hand, BEF research in forests is especially challenging because of the longevity of trees and the difficulty to control environmental factors that co-vary with diversity such as stand age and topography. In this thesis, I examine the effects of tree species richness on aboveground productivity in subtropical China, by using a combination of both experimental and comparative studies.

In the first two chapters, I worked in an ongoing large-scale tree diversity experiment, BEF-China (www.bef-china.de). In a subset of this experiment, over 150,000 tree saplings were selected from a pool of 40 native broad-leaved species and planted in 386 plots, each containing between one to 16 species. In **Chapter 1**, I tested the effect of tree species richness on stand productivity (annual increment of stand basal area) by analyzing data of four annual inventories since the establishment of the experiment (ca. 5000 individuals). I observed the gradual emergence of a positive effect of species richness on stand productivity. Neither spatial heterogeneity nor functional diversity affected stand productivity. However, the presence of two fast-growing species, *Choeropondias axillaris* and *Schima superba*, explained a significant proportion of the variability of stand productivity. Furthermore, I observed that at this stage of stand initiation, mortality (as mortality rate or loss of biomass) was not affected by species richness. In contrast, survivor growth increased with species richness. Thus, this study demonstrates that even during the initial stages of stand development, diversity enhances stand growth.

In **Chapter 2**, I investigated the effects of tree species richness on leaf production. Leaf production is an important component of primary productivity in early stages of forest succession. During stand initiation light availability decreases, and trees can potentially adjust their leaf production, leaf size and branching patterns to those changes in light regime. Therefore, I expected that trees growing in mixtures would show not only larger stems but also higher leaf production. During a two-year study period (3 and 4 years after the establishment of the experiment), I monitored the growth of ca. 700 trees in 62 plots, encompassing a diversity gradient from one to 16 species. I assessed stem basal area, total number of leaves, leaf emergence rate, leaf mortality rate, leaf size, and branching rate. At the end of my study period, trees growing in mixtures, especially those of *C. axillaris*, had larger basal area and longer leaves, but species richness had no effect on any other trait. Thus, this study shows that tree species richness enhances stem growth but not leaf production during stand initiation. The results suggest then that the complementary use of light is not a main driver of increased productivity in mixtures.

In **Chapter 3**, I tested the effects of tree richness on wood production and stand leaf area in a secondary mixed broad-leaved forest. Although the complementary use of the canopy space through light partitioning is often considered the main mechanism of the diversity-productivity relationship, few studies have tested the effect of diversity on the leaf fraction. I hypothesized that more diverse stands, with regards to both species ad functional traits, will develop multi-layered canopies and consequently have higher stand leaf area. Along a gradient of successional age and tree species richness, I estimated stand basal area and its 4-year increase, stand leaf area, and variability in tree heights as measure of vertical space use in 25 plots. Diversity enhanced vertical space use, stand basal area, and stand growth; it did not, however, affect stand leaf area. Thus, the results suggest that changes in aboveground productivity are not mediated by leaf area changes in our study site.

In summary, my results demonstrate that tree species richness enhances stand productivity in experimental and semi-natural stands. The findings highlight the importance of diversity not only as a conservation target but also as a management strategy. This is particularly relevant for forestry policies in China, where species-poor forest plantations are a prevalent strategy of carbon sequestration.

Contents

Introduction

Several studies have reported that biodiversity can enhance primary productivity and other ecosystem functions. Therefore, biodiversity can provide many services to people, and its current loss poses a major threat to human welfare (Millennium Ecosystem Assessment, 2005). In this context, it is crucial to understand the relationship between diversity and ecosystem functioning in forests, which provide services that are vital for our livelihoods but are under threat by land-use conversion, fires, and illegal logging, among others (FAO, 2010). In this thesis, I examine the effect of species richness on primary productivity in subtropical China and explore the possible mechanisms underlying this relationship.

Biodiversity loss

Biodiversity is declining rapidly throughout the world. Driven by the impacts of human activities species loss rate is so high that we are currently on pace to a new mass extinction (Dirzo & Raven, 2003; Barnosky *et al.*, 2011; Alroy, 2015). The loss of diversity, encompassing reductions in number of species, range of functional traits, or range of genotypes, diminishes the efficiency of communities to capture resources, produce biomass, decompose organic matter and recycle nutrients (reviewed by Hooper *et al.*, 2005; Cardinale *et al.*, 2012; Naeem *et al.*, 2012). As a consequence, the provisioning and regulating services of ecosystems (e.g. food and wood provision, climate regulation, pest control) can be significantly impaired (Cardinale *et al.*, 2012; Naeem *et al.*, 2012). In fact, the biodiversity crisis is currently considered a threat to human welfare, comparable to climate change (Rockström *et al.*, 2009; Steffen *et al.*, 2015). It is therefore urgent to better understand the diversity effects on the functioning of ecosystems and the mechanisms underlying such effects.

Biodiversity and ecosystem functioning (BEF) in forests

The need to understand biodiversity and ecosystem functioning (BEF) relationships is especially acute in forest ecosystems, which are of major importance at the global scale. The world's forests cover over 4 billion hectares (31% of total land area) and provide numerous cultural, economical (e.g. timber, food, fuel and bioproducts) and ecological services (e.g. soil and water conservation, avalanche control, and desertification control) (FAO, 2010). Nevertheless, research on BEF in terrestrial ecosystems has been almost exclusively restricted to temperate grasslands, whereas forests have received relatively little attention (Balvanera *et al.*, 2006; Nadrowski *et al.*, 2010).

To date, a positive effect of tree diversity on productivity has been inferred mostly from observational studies using forest plantation or long-term inventory data. For example,

a meta-analysis of tropical and temperate tree plantations (Piotto, 2008) showed that mixture plantations are more productive than monocultures. Furthermore, diversity has a strong and positive effect on tree productivity in non-managed temperate and boreal forests in Canada (Paquette & Messier, 2011). Similarly, the production of tree biomass, soil carbon storage, berry production, and game production potential increases in more diverse boreal and temperate forests in Sweden (Gamfeldt *et al.*, 2013). Likewise, wood production is 24% higher in mixed than in mono-specific forests across Europe (Vilà *et al.*, 2007).

These large-scale observational studies have played a seminal role in the advancement of BEF research in forest. We have learned not only that productivity increases with richness, but that the shape of this relationship can vary among biomes (Paquette & Messier, 2011) and spatial scale (Chisholm *et al.*, 2013). We have also learned that no single species can simultaneously sustain multiple ecosystem services (Gamfeldt *et al.*, 2013), and that diversity promotes temporal stability of wood production in forests (Jucker *et al.*, 2014a). Moreover, a main advantage of observational studies using tree inventory data is their generality and representativity (Nadrowski *et al.*, 2010). Their results reflect real existing forest stands, and can be applied to develop solutions for forest management.

On the other hand, observational studies have some drawbacks. First, most of these studies have been carried out in relatively species-poor forest so far. For example, in one study only 1.5% of the plots contained more than five species (Gamfeldt *et al.*, 2013). Similarly, the temperate and boreal plots analyzed by Paquette & Messier (2011) had on average 3 and 5 species, respectively. Thus, the results likely cannot be extrapolated to more diverse regions. Second, observational studies can not fully control for any of the factors which typically co-vary with tree species richness, e.g. stand age, soil fertility, land-use history or habitat heterogeneity (Scherer-Lorenzen *et al.*, 2005). Third, observational studies have a limited capacity to elucidate the causal mechanisms underlying the BEF relationship (but see Jucker *et al.*, 2015).

Therefore, to advance BEF research in forests it is important first to broaden the geographical scope of observational studies to tropical and subtropical biomes. Second, observational studies should be complemented with experiments, where communities are artificially assembled and diversity is manipulated while environmental variables are kept constant (Scherer-Lorenzen *et al.*, 2005).

Mechanisms underlying the BEF relationship in forests

The effects of biodiversity on ecosystem functioning are explained through three ecological mechanisms: niche differentiation, facilitation among species, and selective processes (e.g. interspecific competition). The first two lead to an increase in resource use in more diverse communities (complementarity effect), while interspecific competition results in one or few species with particular traits dominating a mixture and affecting ecosystem process (selection effect). The non-mutually exclusive selection and complementarity effects can be quantified using the additive partition method (Loreau & Hector, 2001). This method has been widely used in grasslands studies, showing that the complemen-

tarity effect is the main mechanism behind the BEF relationship (Hector *et al.*, 1999; Tilman *et al.*, 2001; Fargione *et al.*, 2007; Marquard *et al.*, 2009; Reich *et al.*, 2012) and that it increases through time (Cardinale *et al.*, 2007; Reich *et al.*, 2012). However, the selection and complementarity effects are in fact statistically defined processes and cannot be directly link to any ecological mechanisms (Petchey, 2003; Fox, 2005). In fact, there are few grassland studies that have explained how the diversity effect is related to population dynamics, such as increased individual size or increased density of individuals (but see Roscher *et al.*, 2007). This gap of knowledge is explained by the difficulty to identify unique individuals due to the clonal growth of many grassland species and the intermingling of neighboring roots and leaves.

In contrast to grasslands experiments, each tree individual can be tracked throughout the duration of the experiment allowing to monitor individual tree growth, mortality and recruitment. These three demographic processes will define the net biomass and its growth (in a time interval) (Clark *et al.*, 2001) and are potentially affected by species richness. To date, there are only a few studies on this topic, but it has been observed that individual growth is enhanced by diversity in the tropics and subtropics (Potvin & Gotelli, 2008; Baruffol *et al.*, 2013).

A key question in BEF research is which ecological processes explain the increase of tree growth in more diverse stands. Species richness can potentially affect both below- and aboveground processes. For example, trees of *Abies alba* (European silver fir) growing in mixture, are less sensitive to drought because interspecific differences in rooting depth lead to an increase in water uptake (Lebourgeois *et al.*, 2013). Similarly, conifer stands containing the N-fixing red alder *Alnus rubra* are more productive than pure conifer stands (Binkley, 2003). The most frequently suggested mechanism underlying the BEF relationship in forests is the complementary use of the canopy through light partitioning. Light competition is widely recognized as a key driver of forest dynamics (Purves & Pacala, 2008; Purves *et al.*, 2008), and higher light availability is linked to higher growth rates (Klinka *et al.*, 1992; Pacala *et al.*, 1994; Chen *et al.*, 1996; Binkley *et al.*, 2010) and to changes in leaf morphology and crown architecture (Petriţan *et al.*, 2009).

To date, few studies have systematically investigated the complementary use of the canopy as a possible BEF mechanism in forests. However, there is increasing evidence of at least three mechanisms: vertical stratification, crown plasticity, and temporal niche differences among species. Morin *et al.* (2011) postulated that if increasing species richness leads to a higher variation in growth ability, tree height and shade tolerance, mixed stands of shade-tolerant and light-demanding species can fill more light niches and develop multilayered canopies. As a consequence of this vertical stratification, the canopy space can be used more completely. On the other hand, trees can adjust their crown morphology in response to competition with neighbors. Recently, Jucker *et al.* (2015) showed that trees have larger crowns when growing in mixtures. Thus, crown plasticity, i.e. intraspecific variation in crown morphology, explains the increase of canopy use efficiency with diversity. Last, in environments where the growth season is not constrained to any particular season, differences in phenology among species could enhance the light capture at stand level, as it has been observed in the Sardinilla tree BEF-experiment in

the Neotropics (Sapijanskas *et al.*, 2014).

Irrespective of the exact mechanism, it is clear that the canopy plays a major role in BEF relationships in forests. The leaves are the site of primary production and an active interface between the forest and the atmosphere. They influence the amount of solar radiation that can be intercepted as well as the plant-atmosphere carbon, water and energy fluxes (Pan *et al.*, 2013). Furthermore, leaf litter production is an important component of net primary productivity, particularly early in succession ($<$ 20 years) (Guariguata & Ostertag, 2001). However, to date most BEF studies have focused on wood production, whereas the effect of species richness on the leaf fraction is still an open question.

BEF-China

In China, forests cover an area of 207 million ha, making the country the fifth one in the world with the largest forest area (FAO, 2010). In the past three decades carbon storage and sequestration have increased (Fang *et al.*, 2001; Shi *et al.*, 2011), and forest is expected to continue to act as a carbon sink at least until 2050 (Xu *et al.*, 2010). This is mainly a result of large-scale national reforestation and afforestation programs (Xu *et al.*, 2010; Shi *et al.*, 2011), which are currently concentrated on monocultures. Managing for diversity could however increase the carbon storage potential. Thus, it is highly relevant to assess how tree diversity maintains ecosystem functions and services.

To shed light on this topic the joint Chinese-German-Swiss research project BEF-China 'The role of tree and shrub diversity for production, erosion control, element cycling, and species conservation in Chinese subtropical forest ecosystems' (www.bef-china.de) was established in 2008. Currently, there are 14 research subprojects, focusing on primary productivity, soil erosion, nutrient cycling, genetic diversity, among others. The BEF-China project includes two methodological approaches: a comparative study in a secondary forest and a large-scale BEF experiment in subtropical China. By combining these two approaches the BEF-China project allows to gain a deeper insight into BEF relationships in the 'real world' and into the causal mechanisms explaining the effect of diversity, respectively. Furthermore, by targeting a subtropical species-rich biome, the BEF-China project contributes to broaden the geographical scope in BEF research in forests.

The comparative study consists of 27 plots covering a gradient of species richness and successional age (Bruelheide *et al.*, 2011). It is located in the Gutianshan National Nature Forest Reserve, Zhejian province, south-east China (29.25 °N, 118.12 °E). The climate is subtropical monsoon, with a mean annual air temperature of 15.1 °C and a mean annual precipitation of 2000 mm. The vegetation is typical of mixed broad-leaved forests. A total of 1462 seed plant species belonging to 684 genera and 149 families are found in the 81 km^2 reserve, with 258 of these species being woody. The reserve covers a mosaic of forest patches in different successional stages, from five to more that 80 years since the last logging event (see Bruelheide *et al.*, 2011, and references therein). By systematically selecting plots that represent different levels of tree species richness within each stand successional age (i.e. time elapsed since the last logging event), the study has more power

to detect causal relationships than conventional sample surveys. In the first phase of the project (2008–2011), Baruffol *et al.* (2013) found that stand basal area and its growth increase with species richness. Although more diverse stands were characterized by a higher abundance of trees and larger tree size, it is not clear yet which mechanism explain the observed BEF relationship.

The BEF-China experiment consists of over 500 (25.8 m × 25.8 m in horizontal projection) plots, where diversity was manipulated by varying the number of species from one to 24. It was established in 2009–2010 near Xinganshan Township, Jiangxi Province, southeast China (29.09 °N, 117.92 °E). The climate is subtropical monsoon, with a mean annual air temperature of 16.7 °C and a mean annual precipitation of 1821 mm (Yang *et al.*, 2013). The natural vegetation corresponds to evergreen broad-leaved forests, characterized by a high tree and shrub species richness (Wang *et al.*, 2007).

Thesis outline

Within the framework of the BEF-China project, I examine the effect of tree diversity on aboveground productivity in subtropical China and explore the possible mechanisms underlying the relationship, both in the comparative study and the large-scale BEF experiment.

In Chapters 1 and 2, I work in the large-scale tree BEF experiment. In **Chapter 1**, I use data from four annual tree inventories to test the effect of tree diversity on stand aboveground productivity in young tree communities. I hypothesize that stand productivity will be higher in more diverse stands. Furthermore, I investigate whether spatial heterogeneity, functional diversity, phylogenetic diversity or the presence of any species influence stand productivity. In addition, I test which component of stand annual growth, i.e. survivor growth, recruitment and mortality, is affected by diversity.

In **Chapter 2**, I test the effects of species richness on leaf production. With the assumption that light conditions vary with diversity and trees can adjust their leaf fraction to changes in the light regime, we hypothesize that trees growing in mixtures will show not only a larger stem size, but also a larger leaf production, smaller leaves and a higher branching rate.

In **Chapter 3**, I continue the work done by Baruffol *et al.* (2013) in the comparative study site. This time, however, I explore a possible mechanism behind the observed increase of stand basal area with species richness. I hypothesize that more diverse stands achieve higher aboveground productivity through a more complete utilization of the canopy vertical space and higher stand leaf area. I estimate stand basal area, stand leaf area and variability in tree heights as measure of vertical space use, and I analyze the effects of species richness on them.

1 Tree species richness enhances stand productivity in a large-scale field experiment in subtropical China

Nadia Castro Izaguirre, Martin Baruffol, Yuanyuan Huang, Bernhard Schmid and Pascal A. Niklaus

Abstract

The increase in plant productivity with species diversity is well documented in temperate grasslands. However, little is known about these effects in forests in (sub)tropical ecosystems, despite their major role in the global cycling of carbon.

Here we tested the effect of tree species richness on aboveground productivity using a large-scale experiment in subtropical China. A subset of this experiment consists of over 150,000 trees planted in 386 plots, containing from one to 16 species. From 2009 to 2013, we monitored basal diameter and height of nearly 5,000 trees. Using mixed-effects models, we tested for diversity effects on stand-level basal area (SBA) and its annual increment, ΔSBA. Furthermore, we tested whether spatial heterogeneity across plots, functional diversity, phylogenetical diversity or the presence of any species explained variability in SBA and ΔSBA. Finally, we tested which component of stand annual growth — survivor growth, recruitment or mortality— was affected by diversity.

We found that ΔSBA increases with species richness in young experimental stands. This effect became evident in the fourth year after the establishment of the experiment, when ΔSBA in the 16-species mixtures was on average 1.8 times larger that in the monocultures. Neither spatial heterogeneity nor functional diversity (after adjusting for species richness) affected ΔSBA. However, the presence of fast-growing species strongly influenced productivity.

Overall, our results demonstrate an effect of diversity on stand aboveground productivity in young tree communities. In this phase, the diversity effects seem largely driven by the successful establishment of fast-growing species.

1.1 Introduction

Two decades of research have confirmed the positive relationship between biodiversity and ecosystem functioning (BEF) in both terrestrial and aquatic environments (reviewed by Hooper *et al.*, 2005; Cardinale *et al.*, 2012; Naeem *et al.*, 2012). Nevertheless, little is known about the BEF relationship in forest ecosystems, which are of major importance at the global scale. The world's forest cover over 4 billion hectares (31% of total land area) and provide numerous functions, e.g. wood and non-wood production, soil and water conservation (FAO, 2010).

To date, several studies have shown a positive effect of tree diversity on productivity in Mediterranean (Vilà *et al.*, 2007), temperate (Paquette & Messier, 2011), boreal (Paquette & Messier, 2011; Gamfeldt *et al.*, 2013) and subtropical (Baruffol *et al.*, 2013) forests. Because most of those studies have been carried out in relatively species poor forest (up to five species), it is uncertain if these results could be extrapolated to more diverse regions. Furthermore, those studies are observational, which limits their potential to elucidate the causal mechanisms, or control for any of the factors which typically co-vary with tree specie richness, namely stand age, soil fertility, land-use history or habitat heterogeneity (Scherer-Lorenzen *et al.*, 2005). This indicates a need to broaden the scope of BEF-research by implementing experiments, where communities with varying species richness are artificially assembled (Scherer-Lorenzen *et al.*, 2005).

An underlying assumption in BEF-research is that species have evolved into different and complementary niches. This way, communities with more species capture more resources and are more productive because of an ecological 'division of labor' (Hector, 2009). Nevertheless, several studies suggest that in species-rich forests diversity is controlled by a combination of niche differentiation (through habitat partitioning or other environmental controls) and neutral processes (Hubbell, 2001; Harms *et al.*, 2001; Legendre *et al.*, 2009; Cheng *et al.*, 2012). If this holds true, the effects of biodiversity loss in species-rich forests would be weak in comparison to grasslands.

A logical consequence of the niche-based assumptions in BEF research is the importance of the diversity of traits in a community (functional diversity, FD) to explain the BEF relation (Hooper *et al.*, 2005; Petchey & Gaston, 2006). In Neotropical young successional forests, for example, the aboveground tree biomass dynamics are correlated to the functional diversity of leaf traits, such as leaf dry matter content and specific leaf area (SLA) (Lasky *et al.*, 2014). However, to identify the relevant functional traits and to measure them can be difficult and time-consuming. If relevant functional traits are phylogenetically conserved, phylogenetic diversity (PD, i.e. the total amount of phylogenetic distance among species in a community) can reflect ecological and functional dissimilarity in a community (Roscher *et al.*, 2007; Srivastava *et al.*, 2012) and can be used as a proxy of FD.

The effect of diversity can also be enhanced by the presence of particular species or functional groups across a range of mixtures, e.g. N-fixing species in forest plantations (Parrotta, 1999; Binkley *et al.*, 2003), and by spatial heterogeneity (Scherer-Lorenzen *et al.*, 2005). In the latter case, individual tree growth can be influenced by slope aspect

(Shen *et al.*, 2014) and soil fertility (Russo *et al.*, 2005).

A widely used method to analyze the mechanisms underlying the BEF relationship is the additive partition method (Loreau & Hector, 2001). The method separates the diversity effect into selection (i.e. result of interspecific competition) and complementarity (i.e. result of niche differentiation and facilitation) effects. The BEF relationship in grassland is mainly caused by complementarity (Hector *et al.*, 1999; Tilman *et al.*, 2001; Fargione *et al.*, 2007; Marquard *et al.*, 2009; Reich *et al.*, 2012), which increases through time (Cardinale *et al.*, 2007; Reich *et al.*, 2012). Nevertheless, little is know how the diversity effect is related to population dynamics, such as increased individual size or increased density of individuals (but see Roscher *et al.*, 2007). Because tree individuals can be tracked through their life cycle, tree experiments represent an opportunity to fill this gap. In forest ecosystems, the combination of growth of surviving trees (survivor growth), mortality and recruitment define the net basal area growth in a time interval (Clark *et al.*, 2001). The effect of diversity on these processes is not clear yet but it has been observed that tree growth (Potvin & Gotelli, 2008) and recruitment (Liang *et al.*, 2007; Young *et al.*, 2011) can increase with diversity, whereas mortality is not affected (Liang *et al.*, 2007; Lasky *et al.*, 2014).

Here we present the results of the BEF-China experiment, a large-scale tree experiment set up in subtropical China to test the effects of tree diversity on primary productivity (www.bef-china.de). Using data from four annual tree inventories, we ask the following questions:

1. Does species richness affect stand productivity in young tree communities? At this stage of our experiment (stand initiation), we expect to observe an overall increase of stand productivity with increasing species richness but no transgressive overyielding (when a mixture outperforms its most productive component monoculture).

2. Do spatial heterogeneity, functional diversity, phylogenetic diversity or the presence of any species affect stand productivity (after adjusting for species richness)? We anticipate that FD, PD, the presence of certain species and some topographic covariates, such as slope inclination and orientation, will explain variation in stand productivity that is not explained by species richness. Because of the young age of our tree stands, we expect early successional species to drive the BEF relationship.

3. Is the diversity effect driven by selection or complementarity effect?

4. Which components of stand annual growth, i.e. survivor growth, recruitment and mortality, are affected by diversity? In the early phase of the experiment, we expect an effect of species richness on survivor growth but not on mortality.

1.2 Methods

We tested the effect of tree species richness on stand productivity in tree communities in a large-scale diversity experiment in subtropical China. Tree communities were established

in 386 plots, where diversity was manipulated by varying the number of species from one to 16.

1.2.1 Study site and experimental design

The experiment was established near Xinganshan Township, Jiangxi Province, south-east China (29.09 °N, 117.92 °E). The climate is subtropical monsoon, with a mean annual air temperature of 16.7 °C and a mean annual precipitation of 1821 mm (Yang *et al.*, 2013). The natural vegetation corresponds to evergreen broad-leaved forests, characterized by a high tree and shrub species richness (Wang *et al.*, 2007).

The experiment consisted of 386 1-mu (25.8 m × 25.8 m in horizontal projection) plots that contain either 1, 2, 4, 8 or 16 tree species. In each plot, 400 tree saplings were planted in a regular grid with 1.29 m distance between individuals. The plots were distributed in two ca. 25 ha sites (A and B) 5 km apart. Site A, established in 2009, has an average slope of 27.5° and its altitude ranges from 107 to 278 m.a.s.l.. In contrast, site B, established in 2010, has a milder topography with an average slope of 31° and an altitude range from 107 to 189 m.a.s.l. Both sites were forest plantations of *Pinus massoniana* and *Cunninghamia lanceolata* that were clear cut before the establishment of the experiment (Yang *et al.*, 2013).

To build the communities we used a pool of 24 native broad-leaved species at each site (40 species in total) (see Table 1.1 for the tree species identities). Only 17 of these species show a preference for a particular stage (either early successional, (n=13), intermediate (n=1) or late (n=3) successional stages), whereas 23 species can be found in two or three successional stages.

Table 1.1: List of species planted in sites A and B of the BEF-China experiment. Species names follow nomenclature in eFloras (2008). Leaf habit: D deciduous, E evergreen. Successional stage (as in Yang *et al.*, 2013, and based on expert knowledge of Prof. M.J. Yu): E early, I intermediate, L late.

Species	Leaf habit	Successional stage	Site
Acer davidii Franchet	D	E/I	A
Ailanthus altissima (Miller) Swingle	D	E/I	B
Alniphyllum fortunei (Hemsley) Makino	D	E/I	B
Betula luminifera H. Winkler in Engler	D	E/I/L	B
Castanea henryi (Skan) Rehd. et Wils.	D	E	A
Castanopsis carlesii (Hemsley) Hayata	E	L	A
Castanopsis eyrei (Champion ex Bentham) Tutcher	E	L	A/B
Castanopsis fargesii Franchet	E	E/I/L	B
Castanopsis sclerophylla (Lindley & Paxton) Schottky	E	E/I/L	A/B

Continued on next page

Table 1.1 – continued from previous page

Species	Leaf habit	Successional stage	Site
Celtis biondii Pampanini	D	E/I	B
Choerospondias axillaris (Roxb.) Burtt et Hill	D	E	A
Cinnamomum camphora (Linnaeus) J. Presl in Berchtold & J. Presl	E	E/I/L	A/B
Cyclobalanopsis glauca (Thunberg) Oersted	E	I/L	A/B
Cyclobalanopsis myrsinifolia (Blume) Oersted	E	I/L	A
Daphniphyllum oldhamii (Hemsley) K. Rosenthal in Engler	E	L	A/B
Diospyros japonica Siebold & Zuccarini	D	E	A/B
Elaeocarpus chinensis (Gardner & Champion) J. D. Hooker ex Bentham	E	E/I/L	B
Elaeocarpus glabripetalus Merrill	E	E/I/L	B
Elaeocarpus japonicus Siebold & Zuccarini	E	I/L	B
Idesia polycarpa Maximowicz	D	E/I	B
Koelreuteria bipinnata Franch.	D	E	A
Liquidambar formosana Hance	D	I	A
Lithocarpus glaber (Thunb.) Nakai	E	I/L	A/B
Machilus grijsii Hance	E	I/L	B
Machilus leptophylla Handel-Mazzetti	E	I/L	B
Machilus thunbergii Siebold & Zuccarini	E	I/L	B
Manglietia fordiana Oliver	E	I/L	B
Melia azedarach Linnaeus	D	E	A
Meliosma flexuosa Pampanini	D	E/I	B
Nyssa sinensis Oliver	D	E	A
Phoebe bournei (Hemsley) Yen C. Yang	E	I/L	B
Quercus acutissima Carruthers	D	E	A
Quercus fabri Hance	D	E	A
Quercus phillyreoides A. Gray	D	E/I/L	B
Quercus serrata Murray	D	E	A
Rhus chinensis Mill.	D	E	A
Sapindus mukorossi Gaertn	D	E	A
Schima superba Gardn. et Champ.	E	E/I/L	A/B
Triadica cochinchinensis Loureiro	D	E	A
Triadica sebifera (L.) Small	D	E	A

Three overlapping sets of 16 species were randomly selected at each site. With each of

these sets, a 16-species community was constructed and randomly divided into two non-overlapping 8-species communities and so on. This so-called 'broken stick design' assures that all species are equally represented at each diversity level and a maximal independence of replicates with respect to composition (Bell *et al.*, 2009).

In addition, monoculture plots of each species were included at every site (24 species growing in monocultures, per site). In total, there were 138 unique communities replicated 1–5 times in a total of 386 plots (Table 1.2). Further details of the design are shown in Bruelheide *et al.* (2014).

Because of the low establishment success of certain species (Yang *et al.*, 2013), replanting of trees was conducted in early spring of 2010-2012 in both sites to replace dead saplings. Further details of the establishment of the BEF-China experiment are given in Yang *et al.* (2013).

1.2.2 Tree size and survival

Because of the large number of plots, our sampling area in each plot (hereafter core area) was restricted to the 16 central planting positions. From 2009 to 2013, at the end of summer or early autumn, we recorded the species, whether the tree was alive or dead, stem diameter at 5 cm above ground (hereafter basal diameter or BD) and height of all individuals in the core area. In the last census (2012 for site A, 2013 for site B) we recorded whether any position in the core area had been replanted with a new sapling, which later allowed us to estimate mortality rates and stand growth components (see below). In total, each site was surveyed four times.

For each plot we calculated the plot abundance as the number of living trees in the core area. In addition, for the last interval (from the third to the fourth inventory) we calculated the mortality rate as the proportion of trees that survived from one census to the next.

For each tree we calculated the stem basal area as $\pi(\mathrm{BD}/2)^2$ and a stem volume indicator as stem basal area$\times$height. Stand basal area (SBA) and stand volume were estimated as the sum of the individual trees' basal area ($\mathrm{m}^2\,\mathrm{ha}^{-1}$) and volume ($\mathrm{m}^3\,\mathrm{ha}^{-1}$), respectively.

Table 1.2: Number of plots per species richness level, community composition and replicates per each unique community composition in the BEF-China Experiment (sites A and B).

Species richness	Community composition	Replicates per community	Total number of plots
1	40	1–5	176
2	48	1–5	112
4	24	1–5	56
8	12	1–5	28
16	6	1–5	14

Stand basal area increment (ΔSBA) and volume increment (ΔVol) were calculated as the increase of stand basal area or stand volume from one census to the next ($m^2\,ha^{-1}\,yr^{-1}$ and $m^3\,ha^{-1}\,yr^{-1}$, respectively).

Since allometric equations for young trees are not available and may depend on diversity, we used SBA and stand volume as proxies of aboveground biomass, and ΔSBA and ΔVol as proxies of yearly aboveground biomass increment, respectively.

To estimate the components of stand growth (survivor growth, recruitment growth and mortality growth) we selected all trees that were alive in the third census and whose planting positions were monitored in the fourth census. Survival growth was estimated as the sum of basal area of all trees that were alive in both census; mortality growth as the sum of basal area of all trees that died during the interval; and recruitment growth as the sum of basal area of all trees that were replanted in the fourth census (in the experiment recruitment is actually caused only by replanting new saplings).

1.2.3 Topographic variables, functional diversity and phylogenetic diversity

Slope inclination and aspect, elevation, latitude and longitude, were obtained from a 5 m digital elevation model (DEM), calculated by ordinary kriging with a nested variogram based on a field campaign dataset (with own differential GPS measurements) (Yang *et al.*, 2013).

To calculate functional diversity sensu Petchey & Gaston (2006) we selected a set of growth-related species traits. Leaf seasonality (evergreen vs. deciduous), specific leaf area (SLA), leaf dry matter content (LDMC), leaf carbon to nitrogen ratio (C:N), and the typical maximum height reached by mature individuals of the species. Data were recorded on individuals sampled in the experimental plots (SLA, LDMC and C:N), or obtained from published literature (Editorial Committee for Flora Reipublicae Popularis Sinicae, 2004). All traits were normalized to zero mean and unit variance; all missing values were set to zero. We generated trait dendograms for these traits, and calculated the total branch length of species occurring in a plot (Baruffol *et al.*, 2013).

We calculated PD based on published sequence information and methods in Baruffol *et al.* (2013). Using a maximum likelihood (ML) method we generated a phylogenetic tree including 40 species present in our experiment. Phylogenetic diversity was then calculated as total branch length defined by the subset of species occurring in a plot.

1.2.4 Overyielding and diversity effects

To asses non-transgressive overyielding we calculated relative yield totals (RYT). The relative yield (RY) of species is its yield in a mixture as a proportion of its yield in monoculture, and the RYT of a mixture is simply the sum of all relative yields of all component species (Harper *et al.*, 1977). Overyielding occurs if RYT$>$1. To assess transgressive overyielding we calculated the deviation (D) of the mixture yield from the yield of its most productive component monoculture (the difference between the observed field of a mixture and the monoculture yield of its most productive component species, divided by the monoculture yield). Transgressive overyielding occurs if D$>$1.

Net diversity effect, selection effect and complementarity effect were calculated following Loreau & Hector (2001). For each species we calculated the monoculture SBA and ΔSBA as the average of the 2–5 monoculture plots per species. If a species was missing in monoculture (i.e. it failed to establish or was not planted), the effects could not be calculated. Thus, all communities containing the missing species were excluded.

1.2.5 Statistical analysis

To test for species richness effects, we analyzed stand basal area (SBA), stand basal area increment (ΔSBA), net diversity effect (NE), selection effect (SE), complementarity effect (CE), and the components of stand growth (survival, recruitment and mortality growth) by fitting linear mixed-effect models. Species richness and site were fixed terms and community composition, the random term. Preliminary analysis showed that the species set used to construct each of the 16-species communities did neither affect SBA (Year 1: $P=0.11$; Years 2–4: $P>0.33$) nor ΔSBA ($P>0.32$ for all years) in any year. Thus, we did not include this term in our models. In the analysis of NE, CE and SE, outliers (±4 SD) were removed prior to the analysis. All calculations and analysis were performed using R Statistical Software (R Core Team, 2015) and the asreml package for mixed-effect models (VSN International, Hemel Hempstead, UK). Means are reported with their standard deviations.

To shed light into the factors influencing the BEF relationship we tested for the effect of spatial heterogeneity, species identity, functional diversity (FD) and phylogenetic diversity (PD) on SBA and ΔSBA. To test the effect of spatial heterogeneity, we added slope inclination, slope aspect (northness and eastness), altitude, latitude and longitude as covariates to our model (after the species richness term). Prior to the analysis, all topographic variables were normalized to zero mean and unit variance. Next, in order to identify the species that may be driving the BEF relationship we added a species presence-absence contrast after the species richness term in our model. We fitted the model for each species and selected the species explaining most variance. Next, we added the selected species term to the model and repeated the procedure with the remaining species until we selected the three species explaining most variance. Likewise, effects of FD and PD were tested after adjusting for effects of species richness (FD or PD fitter after species richness).

To asses the effect of species richness on tree abundance and mortality rate we fitted generalized linear models with a logit link and a complementarity log-log link, respectively. In both cases we accounted for overdispersion, if necessary. For the mortality rate model we calculated the number of days between two census, log-transformed and used it as 'offset' variable (Egli & Schmid, 2001).

1.3 Results

In total, we measured 4715–5075 living trees every year. Tree basal diameter increased from 0.4 ± 0.4 cm in the first census to 2.6 ± 2.0 cm in the fourth census. In the same

period, height increased from 31 ± 28 cm to 168 ± 122 cm. In the last interval, the species with the largest mean basal diameter increase were *Elaeocarpus japonicus*, *Elaeocarpus glabripetalus* and *Choerospondias axillaris*; the species with the lowest mean basal diameter increase were *Machilus leptophylla*, *Celtis biondii*, and *Machilus grijsii*.

At the plot level, we observed a 37–fold increase in the mean SBA from the first to the fourth census (Year 1: $0.09 \pm 0.15\,m^2\,ha^{-1}$; Year 4: $3.38 \pm 3.30\,m^2\,ha^{-1}$), while ΔSBA increased from $0.59 \pm 0.87\,m^2\,ha^{-1}\,yr^{-1}$ to $1.68 \pm 1.60\,m^2\,ha^{-1}\,yr^{-1}$ in the same time interval.

1.3.1 Effect of species richness on tree abundance, SBA and ΔSBA

In our 4-year study period, the mean number of living individuals in the core area varied between 10.8 and 11.1 among years. Tree abundance was not affected by species richness in any year ($P>0.30$). From the first to the third year, tree abundance differed between sites (Year 1: $F_{1,160.93}=71.63$, $P<0.001$; Year 2: $F_{1,9.58}=3.94$, $P<0.05$; Year 3: $F_{1,17.95}=7.94$, $P<0.01$).

During our study period, SBA was not affected by species richness ($P>0.12$ for all years). In the first year, SBA differed between sites ($F_{1,332.4}=26.02$, $P<0.001$). From the first to the third year, the highest SBA values were clearly achieved by monoculture plots (Fig. 1.1).

In the first two census intervals, ΔSBA did not vary with species richness. In the last interval (year 3–year 4), ΔSBA increased with species richness ($F_{1,119}=5.76$, $P<0.05$; Fig. 1.1) and it differed significantly between sites ($F_{1,319}=4.15$, $P<0.05$).

Because results of volume and ΔVol were similar to the ones of SBA and ΔSBA, we report here only the results of SBA and ΔSBA.

1.3.2 Overyielding and transgressive overyielding

The annual proportion of plots overyielding and transgressively overyielding varied between 21–64% and 0-32%, respectively (Table 1.3). Among diversity treatments, 16-species plots showed the lowest proportion of overyielding, whereas 2-species mixtures showed the highest proportion of transgressive overyielding.

1.3.3 Topographic covariates

SBA was affected by altitude, longitude and slope in the first year, the third year, and from the second to the fourth year (altitude: $F_{1,307.1}=8.32$, $P<0.01$ in year 1; longitude: $F_{1,343}=6.10$, $P<0.05$ in year 3; slope: $F_{1,290.9}=4.91$, $P<0.05$ in year 1; $F_{1,316.5}=6.94$, $P<0.01$ in year 2; $F_{1,313.2}=5.084$, $P<0.05$ in year 3).

In the first census interval, ΔSBA was affected by longitude ($F_{1,311.7}=4.01$, $P<0.05$). In the second census interval, ΔSBA was affected by slope ($F_{1,328.6}=6.93$, $P<0.01$) and longitude ($F_{1,316.7}=8.24$, $P<0.01$).

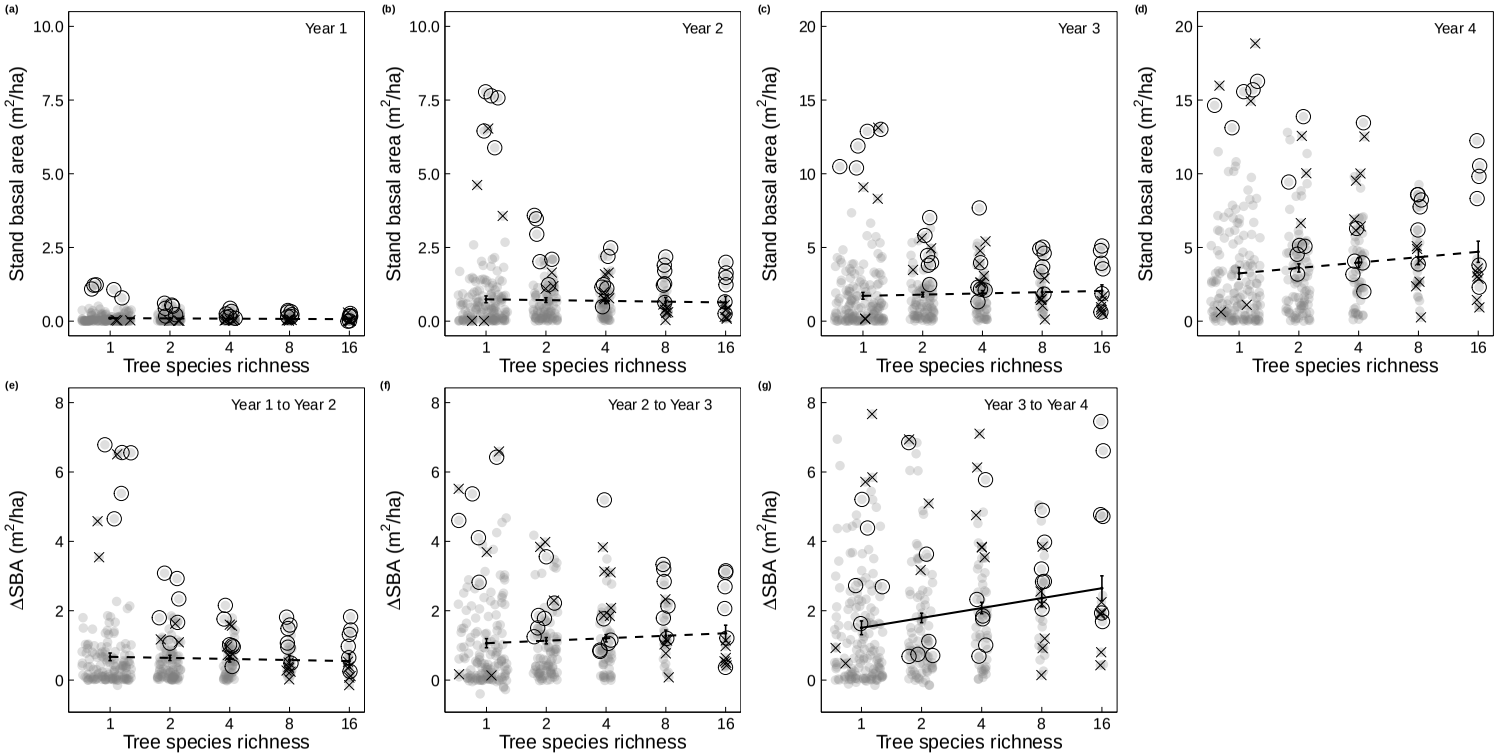


Figure 1.1: SBA (a-d) and ΔSBA (e–g) as a function of species richness, calculated for each census interval separately. The positive effect of richness on ΔSBA became significant in the last census interval. Grey dots indicate values for individual plots; open circles, plots containing *Choerospondias axillaris*; crosses, plots containing *Schima superba*. Black circles and lines show predicted values of the statistical models (see methods).

Table 1.3: Non-transgressive and transgressive overyielding per species richness level and year (since the establishment of the experiment) for stand basal area (SBA) and its increment (ΔSBA). Columns show the percentage of plots that show (transgressive) overyielding and the number of plots (in parenthesis).

Year	Species richness	Non-transgressive overyielding		Transgressive overyielding	
		SBA	ΔSBA	SBA	ΔSBA
1	2	55.79 (53)	45.26 (43)	30.36 (34)	27.68 (31)
	4	45.45 (25)	38.18 (21)	16.07 (9)	8.93 (5)
	8	42.86 (12)	35.71 (10)	0.00 (0)	3.57 (1)
	16	42.86 (6)	28.57 (4)	7.14 (1)	0.00 (0)
2	2	44.21 (42)	36.84 (35)	27.68 (31)	32.14 (36)
	4	42.86 (24)	28.57 (16)	7.14 (4)	12.50 (7)
	8	46.43 (13)	42.86 (12)	0.00 (0)	3.57 (1)
	16	35.71 (5)	42.86 (6)	0.00 (0)	0.00 (0)
3	2	37.90 (36)	45.26 (43)	29.46 (33)	41.07 (46)
	4	41.07 (23)	46.43 (26)	7.14 (4)	23.21 (13)
	8	57.14 (16)	57.14 (16)	3.57 (1)	14.28 (4)
	16	21.43 (3)	71.43 (10)	0.00 (0)	28.57 (4)
4	2	36.84 (35)	32.14 (36)		
	4	37.50 (21)	10.71 (6)		
	8	64.28 (18)	7.14 (2)		
	16	42.86 (6)	0.00 (0)		

1.3.4 Species identity

The presence of *C. axillaris*, *Quercus serrata*, *Cyclobalanopsis myrsinifolia*, *E. glabripetalus*, and *Castanopsis eyrei* affected SBA. Similarly, the presence of *C. axillaris*, *Q. serrata*, *Schima superba*, *E. glabripetalus*, and *Castanopsis eyrei* affected ΔSBA.

SBA and ΔSBA increased with species richness in plots containing individuals of *Q. serrata*, *C. myrsinifolia* and *C. eyrei* (data not shown). In contrast, SBA and ΔSBA decreased with species richness in plots containing *E. glabripetalus* and *S. superba*. Plots with *C. axillaris* showed a similar pattern until the last year, when ΔSBA was higher in the 16-species plots.

1.3.5 Phylogenetic and functional diversity

Neither FD nor PD could explain any additional variance for SBA or ΔSBA in any year ($P>0.16$ when fitted after the species richness term).

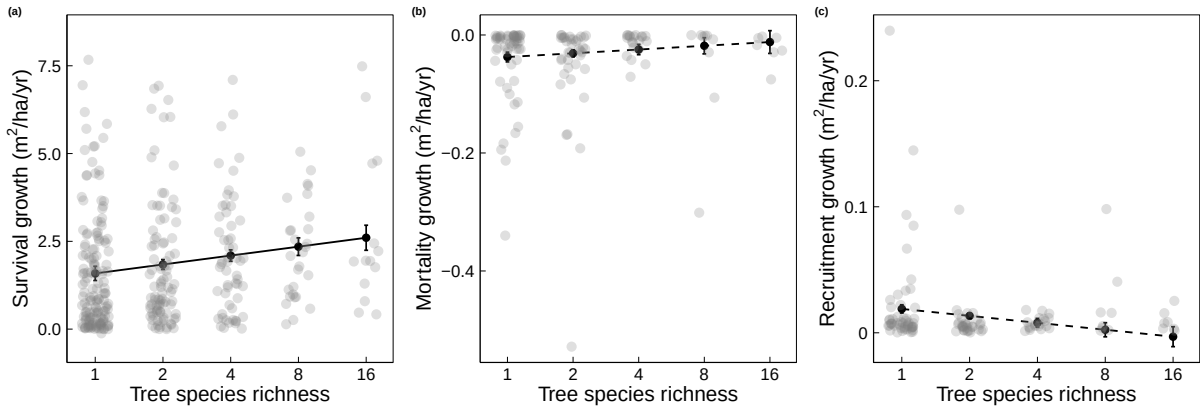


Figure 1.2: Components of stand growth as a function of species richness. Survival growth (a), mortality growth (b) and recruitment growth (c) in the last year interval. Survival growth increased significantly with richness. Grey dots indicate values for individual plots; black circles and lines show predicted values of the statistical models (see methods).

1.3.6 Selection and complementarity effect

For ΔSBA, NE increased with increasing species richness in the last two intervals (year 2–year 3: $F_{1,66.6}$=5.09, P<0.05; year 3–year 4: $F_{1,64.1}$=6.73, P<0.05); only in the last interval, its grand mean (across all species richness levels) was different from zero ($F_{1,60.0}$=6.29, P<0.05).

In the last two intervals, the average SE was larger than zero (Year 2–Year 3: $F_{1,53.3}$=6.31, P<0.05; Year 3–Year 4: $F_{1,46.0}$=4.74, P<0.05) but it was not affected by species richness (P>0.36 in both intervals).

In contrast, CE values in the first interval were on average negative ($F_{1,51.8}$=5.31, P<0.05) and decreased with species richness ($F_{1,51.4}$=6.74, P<0.05). In the second interval, CE on average was still negative ($F_{1,62.4}$=9.58, P<0.01) but did not change with species richness (P>0.77). In the third interval, CE increased with increasing species richness but the effect was only marginally significant ($F_{1,60.2}$=3.19, P<0.10), and CE's grand mean was not significantly different from zero ($F_{1,59.5}$=3.22, P<0.10).

1.3.7 Components of stand growth and mortality rate in the last interval

In the last year the average survival growth was $1.79 \pm 1.70\,m^2\,ha^{-1}\,yr^{-1}$ and increased with species richness ($F_{1,116.2}$=4.50, P<0.05). The average mortality and recruitment growth were $0.04 \pm 0.07\,m^2\,ha^{-1}\,yr^{-1}$ and $0.01 \pm 0.03\,m^2\,ha^{-1}\,yr^{-1}$, respectively. None of them was affected by species richness (Fig. 1.2).

Plots in site B had on average a higher survival growth and recruitment than plots in site A (survival growth: $F_{1,298.2}$=4.03; recruitment growth: $F_{1,49.1}$=6.41, P<0.05). Mortality rate (in the last year) was not affected by species richness (P>0.05).

1.4 Discussion

We found that stand growth increases with species richness in young experimental stands. To our knowledge, our study is the first one to detect this relationship in the subtropics, using a large diversity gradient (from one to 16 species) and multiple replicates for each species richness level. The effect of species richness became evident in the fourth year after the establishment of the experiment, when ΔSBA was on average 1.8 times larger in the most diverse plots (16 species mixtures) than in the monocultures. At the same time, ca. 40% and 20% of our plots showed non-transgressive and transgressive overyielding, respectively. The observed overyielding rate is lower than values observed in grassland experiments (e.g. 40-50% in Roscher *et al.*, 2005). However, the result suggests that resource partitioning, facilitation or other mechanisms, e.g. reduction of natural enemy impacts, are occurring in our mixtures.

1.4.1 Effect of richness on stand productivity

In contrast to results from previous tree BEF experiments, the effect of species richness was linear at plot level. In the Sardinilla experiment in Panama, for example, tree growth in mixtures was higher than in monocultures but it was not affected by the number of species in the mixtures. Potvin & Gotelli (2008) suggested that the species richness of local neighborhoods (i.e. heterospecific vs conspecific individuals) is more relevant to tree growth than species richness at stand level.

In comparison to the biodiversity effects in natural or semi-natural forests, the effect size of diversity in our experiment is small (normalized effect size Zr=0.22). As an example, in a comparative study in a nearby forest, Baruffol *et al.* (2013) observed a 62% increase in stand growth when increasing species richness from 10 to 20 (after adjusting for successional age), and the normalized effect sizes Zr varied between 0.44–0.81. However, since the stands in our study site are still very young and many of them have not reached yet canopy closure, we expect to see more intra- and interspecific interactions and a larger richness effect in the next years.

1.4.2 Other factors affecting stand productivity

Environmental variables can play a major role in tree experiments, specially in heterogeneous and hilly landscapes like ours. In the Sardinilla experiment, for example, topographic traits, such as slope, absence of ditches and elevation, can explain as much as or more variability in stand growth than species richness (Healy *et al.*, 2008). In our site, trees growing in south-facing slopes showed a higher growth than those growing in north-facing slopes (Li *et al.*, 2014). Contrary to our expectations, the topographic effect on tree individual growth was not translated into an effect at stand level, and no single topographic variable affected stand productivity in all years. These results are, however, consistent with those of Baruffol *et al.* (2013) who found that topographic covariates explained less than 1% in the variability of stand growth in a nearby forest.

The presence of certain species can enhance or diminish the productivity of a community

and thus affect the BEF relationship. For example, in the Sardinilla experiment, the presence of *Cedrela odorata*, a productive timber species, and *Anacardium excelsum*, a species that allocates a large proportion of its biomass to branches, are associated with high and low productivity (along all the diversity treatments), respectively (Healy *et al.*, 2008). Here, we found that six species could explain the variability in the relationship between species richness and stand productivity: *Castanopsis eyri*, *Quercus serrata*, *Cyclobalanopsis myrsinifolia*, *Choerospondias axillaris*, *Elaeocarpus glabripetalus*, and *Schima superba*. Plots where any of first three species was present, showed an increase in stand productivity with species richness. Individual growth of these species was poor in our study site (Li *et al.*, 2014), and two of them, *C. eyri* and *C. myrsinifolia* are evergreen, late-successional and shade-tolerant species (Yang *et al.*, 2013; Cheng *et al.*, 2014), whose low performance is probably due to the high light availability in our sites that were clear cut just before the experiment establishment. We hypothesize that the impact of these unproductive species is proportional to its abundance, i.e. the more diverse a plot is, the less frequent this species occurs and its negative impact is attenuated by the presence of more productive species.

On the other hand, *C. axillaris*, *E. glabripetalus* and *S. superba* are very productive species that showed a high individual growth (Li *et al.*, 2014) and a high stand basal area when growing in monocultures (data not shown). In the case of *S. superba*, high temperatures and light intensity can enhance photosynthesis rates in saplings (Guchou *et al.*, 2007). Thus, this sun-adapted species probably benefited from the rich light conditions in our study site. Likewise, *C. axillaris* is a light-demanding species that shows a high survival and growth rate in open areas (Pakkad *et al.*, 2003). Although *E. glabripetalus* is an evergreen species typical of late successional stages (Böhnke & Bruelheide, 2013; Xiang *et al.*, 2013), it can grow in early and intermediate stages too (M. Yu, pers. comm.). Overall, plots with any of these species showed a negative relationship between species richness and stand productivity. A possible explanation is the higher relative abundance and resulting higher summed basal area of these species in low diversity plots.

Interestingly, in the last census interval the relation between species richness and stand productivity in plots with *C. axillaris* changed from negative to positive. In this case, we hypothesize that the intraspecific competition became so high in monocultures that individual growth was diminished, while individuals growing in mixtures benefited from the reduced intraspecific competition. In our study site, individual growth decreased with increasing size of the neighboring trees (Li *et al.*, 2014). An analysis at individual level could determine if the higher individual growth rates of *C. axillaris* were achieved at the expenses of less productive species or not.

Contrary to our expectations, the addition of functional diversity as covariates in our model did not explained more variance in the stand growth in the last census interval. This result may be explained by the fact that most of the species we used can be naturally found in early successional forests. Therefore, since our experiment was not designed to manipulate functional diversity, it is quite likely that these species share similar functional traits and that the gradient of functional diversity within each species richness level is too narrow to explain any variance. Another possible reason is the misidentification of the

relevant functional traits. Indeed, functional traits vastly changed during succession in a Neotropical forest (Lasky *et al.*, 2014).

1.4.3 Selection and complementarity effects

Through our study period we observed that the complementarity effect changed from having a negative overall mean and a negative relationship with species richness to having (marginally significant) positive ones. This result suggests that positive interspecific interactions are driving the diversity effect on stand growth in the last interval. This is an unexpected result because our species identity analysis suggests a 'sampling' or selection effect, where highly productive species dominate the mixtures. It is important to consider that the selection and complementarity effects are statistically defined processes and do not correspond to any ecological mechanism, e.g. resource partitioning, facilitation or interspecific competition. In addition, although this method has been successfully used to analyze long-term grassland experiments, it might not be appropriate for young tree experiments, like ours. Grassland experiments are usually long-term and allow drastic changes in species relative-abundance (Petchey, 2003). In contrast, the mean tree abundance and species composition in plots in our site have remained relatively constant among years. Thus, analysis of tree demographics and performance would be probably more helpful to explain the mechanisms underlying the effect of richness at stand level.

1.4.4 Components of stand growth

An objective of this study was to determine which component of stand growth was affected by species richness. We found that the survival growth was by far the largest component and the only one that increased with species richness. In contrast, the loss and gain of stand basal area due to mortality and recruitment, respectively, were similar among all levels of species richness. These result match those observed in the Sardinilla experiment, where tree diversity enhanced the stand basal area by an increase in individual growth whereas mortality remained constant in young forest stands (Potvin & Gotelli, 2008). Although mortality rates are not affected by species richness and its effect on stand growth is minimal, in certain monocultures stands, as the ones of *C. axillaris*, the high intra-specific competition seems to be slowing down the individual growth. We suggest that in the next years, increasing competition (either intra- or interspecific) will lead to self-thinning and consequently mortality will play a more important role in shaping the BEF relationship.

1.4.5 Conclusions

Overall, our study shows a positive effect of diversity on stand basal area of subtropical tree communities already during the initial stages of stand development. In this phase, the diversity effects seem largely driven by the successful establishment of a fast-growing species, *C. axillaris*. Our results suggest that the intraspecific competition is so high in monocultures of this species that individual growth is diminished.

Our findings are relevant for forestry policies in China, where national reforestation and afforestation programs have contributed to the increase of carbon storage and sequestration in the past three decades (Xu *et al.*, 2010; Shi *et al.*, 2011). However, most of these programs are concentrated on monocultures. Thus, we consider that managing for forest diversity will be an important mitigation effort to effectively increase carbon storage.

2 Tree diversity enhances stem growth but not leaf production in a large-scale field experiment in subtropical China

Nadia Castro Izaguirre, David Emmerth, Zhenkai Sun, Keping Ma, Pascal A. Niklaus and Bernhard Schmid

Abstract

Wood production increases with tree species richness, but whether leaf production shows the same pattern is not clear yet. Leaf production is an important component of primary productivity in early stages of forest succession. During stand initiation light availability decreases, and trees can potentially adjust their leaf production, leaf size and branching patterns to those changes in light regime. Here, we investigated the effect of species on individual growth, both in the wood and leaf fraction. With the assumption that light conditions vary with species richness and that trees can adjust their leaf fraction to changes in light regime, we hypothesize that trees growing in mixtures would show not only larger stems but also higher leaf production.

In a 2-year study period we monitored tree basal area, leaf production, leaf size, and branching patterns of ca. 700 trees in a experimental site in subtropical China. The experiment consisted of 62 plots, each containing 400 planted saplings and from one to 16 species. Leaf production was assessed using three proxies: the total number of leaves in each tree, leaf emergence and leaf mortality rates of marked cohorts.

At the end of the study period, trees growing in mixtures had larger basal area and longer leaves. In contrast, species richness had no effect on leaf emergence rate, leaf mortality rate, the total number of leaves, or branching rate. The effects of species richness were particularly observed in *Choroespondias axillaris*, a fast-growing species with compound leaves.

Overall, our study demonstrates that species richness enhances stem growth but not leaf production during stand development. At this stage, the diversity–growth relation is mainly driven by *C. axillaris*, which suggests the predominance of selection effects. The uncoupled response of leaf and woody components suggests that the complementary use of the canopy space through light partitioning is not a (main) driver of increased productivity at higher species richness.

2.1 Introduction

Several studies have shown that stand wood production increases with tree species richness (Vilà *et al.*, 2007; Paquette & Messier, 2011; Gamfeldt *et al.*, 2013; Baruffol *et al.*, 2013). In contrast, few studies have investigated the relationship between species richness and leaf production (but see Jacob *et al.*, 2010; Seidel *et al.*, 2013), particularly in young stands. Given the increase in secondary forests and plantations, and their role in carbon sequestration (FAO, 2010), it is relevant to understand the effect of diversity on productivity in the early stages of stand development.

Although wood production is the most visible component of tree growth, leaf production is also an important component. Early in succession ($<$ 20 years), net primary productivity is dominated by leaf litter production rather than by wood production (Guariguata & Ostertag, 2001). In addition, leaves are functionally important because they intercept light and assimilate carbon through photosynthesis. Studies on secondary succession have shown that as stand basal and leaf area increase during succession, less light reaches the forest floor (Selaya *et al.*, 2008) and competitive interactions for light become more important than environmental filtering (Lohbeck *et al.*, 2014). It is expected therefore that any increase of tree biomass with increasing species richness may be linked to changes in the light regime and the canopy fraction in young stands.

To respond to changes in light regime trees can adjust their biomass allocation to shoots, their leaf morphology, and their branching patterns. At low irradiance woody plants, both sun- and shade-tolerant species, allocate more biomass to the leaf fraction to maximize light capture (Poorter *et al.*, 2012). Similarly, leaf turnover responds to light conditions; evergreen rainforest species, irrespective of their native habitat i.e. late primary or early secondary successional communities, had a longer lifespan when grown in shaded environments (Reich *et al.*, 2004). Furthermore, high leaf turnover rates are typical of short-lived pioneer species that dominate early secondary successional forest communities (Selaya *et al.*, 2008).

Leaf size is another important trait that can affect self-shading and consequently whole-plant light capture (Falster & Westoby, 2003). In tropical forests, although leaf size plasticity is limited, sun trees have smaller leaves than conspecific shade ones, probably to prevent leaf overheating (Rozendaal *et al.*, 2006; Poorter & Rozendaal, 2008).

An additional mechanism for dealing with a change in light conditions is through modifications in branching patterns, which influence the packing and exposure of leaves (Niinemets, 2010). An increase in light availability may increase branching rate (i.e. the number of branches per unit mother shoot) resulting in a denser 'multilayer canopy' (Niinemets, 2010, and references therein).

In a previous study we found that stand wood production increased with tree species richness, whereas mortality and tree abundance remained constant in a 4-years old biodiversity-ecosystem functioning experiment in subtropical China (BEF-China, www.bef-china.de) (Chapter 1). Here we tested the effect of species richness on the leaf fraction in year three and four after the experiment was established. With the assumption that light conditions vary with diversity, we hypothesize that trees growing in mixtures will show not only a

larger stem size, but also a larger leaf production, smaller leaves and a higher branching rate. Furthermore, we expect to observe a gradual emergence of the species effect as stands develops during our 2-years study period.

2.2 Methods

2.2.1 Study site and experimental design

We studied the response on tree growth of tree species richness in a large-scale diversity experiment in subtropical China, the BEF-China project (www.bef-china.de), during two growing seasons in 2011 and 2012. The experiment was established in 2009 near Xinganshan Township, Jiangxi Province, south-east China (29.09 °N, 117.92 °E), with 512 1-mu (25.8 m × 25.8 m in horizontal projection) plots, spanning a tree diversity gradient of 1 to 24 native broad-leaved species. The climate is subtropical monsoon, with a mean annual air temperature and precipitation of 16.7 °C and 1821 mm, respectively (Yang *et al.*, 2013). The natural vegetation include evergreen broad-leaved forests, characterized by a high tree and shrub species richness (Wang *et al.*, 2007). (For a detailed description of the experimental design see Bruelheide *et al.*, 2014).

The current study focused on a subset of 62 plots planted with 1, 2, 4, 8 or 16 native deciduous and evergreen broad-leaved tree species (see Table 2.1 for the tree species identities). In each plot, 400 tree saplings were planted in a regular grid with 1.29 m distance between individuals. Communities were built following a 'broken stick design'. Specifically, a 16-species community was randomly divided into two non-overlapping 8-species communities, which were similarly divided into two non-overlapping 4 species communities. The process was repeated to obtain 2 species communities and monocultures. This design ensures that all species are equally represented at each diversity level and a maximal independence of replicates with respect to composition (Bell *et al.*, 2009). We included 31 unique community compositions in our study and each species composition was replicated in two plots. Because of the low establishment success of certain species, e.g. *Castanopsis eyrei*, *Cyclobalanopsis myrsinifolia*, dead saplings were replaced with saplings of equal size in early spring of 2010–2012 (see Yang *et al.*, 2013, for details of the establishment of the BEF-China experiment).

In 2011 and 2012 we measured stem, leaf and branch traits (Table 2.2) to assess aboveground tree growth for the 16 central tree planting positions (core area) of each plot. Trees that were replanted in 2011 and 2012 or that died in the course of our study were excluded from all analysis.

2.2.2 Stem size

In early spring and late summer of 2011 and 2012 (i.e. start and end of the growing season) we recorded species identity and measured stem diameter at 5 cm above ground (hereafter basal diameter or BD) of all individuals in the core area. We calculated the stem basal area as $\pi(BD/2)^2$ in each census (i.e. spring 2011, summer 2011, spring 2012, summer 2012) for each tree.

Table 2.1: Tree species planted in the BEF-China experiment. Species names follow nomenclature in eFloras (2008). Leaf habit: D deciduous, E evergreen. Successional stage (as in Yang *et al.*, 2013): E early, I intermediate, L late.

Species	Leaf habit	Successional stage
Castanea henryi (Skan) Rehd. et Wils.	D	E
Castanopsis eyrei (Champion ex Bentham) Tutcher	E	L
Castanopsis sclerophylla (Lindley & Paxton) Schottky	E	E/I/L
Choerospondias axillaris (Roxb.) Burtt et Hill	D	E
Cyclobalanopsis glauca (Thunberg) Oersted	E	I/L
Cyclobalanopsis myrsinifolia (Blume) Oersted	E	I/L
Koelreuteria bipinnata Franch.	D	E
Liquidambar formosana Hance	D	I
Lithocarpus glaber (Thunb.) Nakai	E	I/L
Nyssa sinensis Oliver	D	E
Quercus fabri Hance	D	E
Quercus serrata Murray	D	E
Rhus chinensis Mill.	D	E
Sapindus mukorossi Gaertn	D	E
Schima superba Gardn. et Champ.	E	E/I/L
Triadica sebifera (L.) Small	D	E

2.2.3 Leaf production

Leaf production is usually estimated by a combination of harvest-based allometric equations and liter collection methods. In our study the challenge was firstly the lack of allometric equations for the size range of the trees. The second challenge was the unsuitability of litter traps for forests in which the crown bases are in such close proximity to the ground level. We therefore used a combination of alternatives methods to estimate leaf production.

In the late summer of 2011 and 2012, we counted the number of leaves in 1–5 branches, so that it added up to nearly 150 leaves. Using this value as a reference, we did a visual estimation of the total leaf number for the tree, which we used as a proxy for leaf production.

To assess increases (leaf emergence rate) and reductions (mortality rate) in leaf production we tracked marked leaf cohorts on the tree individuals in the core area during 2011 and 2012. We randomly selected one midcrown branch per individual in May 2011, counted the leaves and marked the base and the tip of the branch with colored wire (above the newest leaf). In August 2011 we counted the number of dead and new leaves.

In April 2012 again we selected one branch per individual and followed the same methodology as in 2011. Plots were revisited multiple times, every 12–173 days until May 2013

Table 2.2: List of parameters measured in this study. Parameters are related to stem size, leaf production, leaf size and branching pattern. Columns show their definition and how many times they were measured in 2011 and 2012.

Variable	Definition	Measuring frequency
Stem size		
Basal area	Basal area (at 5 cm above ground)	Early spring and late summer 2011 and 2012 (4 times)
Leaf production		
Total number of leaves	Number of leaves in each tree at the end of summer	Late summer 2011 and 2012 (2 times)
Leaf emergence rate	Number of new leaves by number of leaves in previous cohort	Late summer 2011 (1 time) Early spring 2012 to early spring 2013 (6 times)
Leaf mortality	Number of dead leaves by number of surviving leaves at the beginning of the interval	Late summer 2011 (1 time) Early spring 2012 to early spring 2013 (6 times)
Leaf size		
Leaf length	Length from the petiole attachment to the tip of the leaf	Late summmer 2011 and 2012 (2 times)
Branching pattern		
Branching rate	Number of sidebranches per number of leaves in cohort	Late summer 2011 and 2012 (2 times)

(a total of 389 days). At each visit, we counted the number of dead and new leaves since the previous census, and remarked the branches at the tip. This was done in order to define cohorts, i.e. all leaves that emerged during each census interval, and assess how age or time of emergence influenced demographic rates.

Leaf emergence rate was estimated for each branch and interval as the number of new leaves produced at the end of the interval divided by the number of leaves in the previous cohort and the duration (in days) of the interval. New leaves were assumed to have emerged at the midpoint of the interval prior to the observation.

Leaf mortality rate was estimated for each cohort and census interval by dividing the number of dead leaves in each interval by the number of surviving leaves at the beginning of each interval. In 2011 therefore we recorded only one measurement for each tree, whereas in 2012 we recorded 4 or 6 measurements for deciduous and evergreen trees, respectively.

2.2.4 Leaf size

In the late summer of 2011 and 2012, we randomly selected one of the newly emerged leaves and measured its length from the petiole attachment to the tip of the leaf (single leaves) or to the most distant leaflet (pinnate leaves).

2.2.5 Branching pattern

In 2012 we assessed branching patterns by counting the number of new branches emerging from each cohort (side-branches) during each plot visit. Only side branches with fully expanded leaves were considered. Branching rate refers to the highest number of side branches of a given cohort (at any time interval) by the initial number of leaves in same cohort.

2.2.6 Statistical analysis

To test the effect of richness on stem size, leaf production, leaf size, and branching patterns we used linear and generalized linear mixed-effect models (GLMMs). We included as random terms community composition, plot and their interactions. Since interspecific differences in all traits were expected, species was included as a fixed term in all our models. Species is a characteristic at individual or at plot level depending on whether the tree is planted in a mixture or monoculture, respectively. To test the effect of species at the correct level, we included a contrast term between monocultures and mixtures ('monomix'), and two new species terms, 'monospecies' and 'mixspecies'. In monospecies, all individuals growing in monocultures were referred to by species name, whereas all individuals growing in mixtures were merged into a single category: 'mix'. The opposite was done for the mixspecies term. The fixed terms were then fitted in the following order: monomix, monospecies, richness and mixspecies.

Basal area, total number of leaves, leaf emergence, leaf size, and branching rate were analyzed using linear-mixed effect models. Data was transformed using a 0.25 exponent.

Leaf mortality was modeled assuming a binomial error distribution and using a complementary log-log link function. Because leaf mortality is expected to increase with cohort age and date of the growing season, cohort age and census date were included as fixed terms. In addition to community composition and plot, random terms included tree and cohort. The number of days between two censuses was log-transformed and used as an 'offset variable' (Egli & Schmid, 2001). Given that cohort age and census date could potentially mask or enhance the richness effect, both terms were fitted either before or after the term richness.

All calculations and analysis were performed using R Statistical Software (R Core Team, 2015) and the asreml package for mixed-effect models (VSN International, Hemel Hempstead, UK). Means are reported with their standard deviations.

2.3 Results

In total, we monitored 687 and 699 living trees in 2011 and 2012, respectively. One species, *Castanopsis eyrei*, was excluded from the analysis because no surviving individuals was present in the core area. Stem size and leaf length in 2012 increased with an increase in species richness. In contrast, for all other measured traits, we found no statistical evidence of an effect of species richness. As expected, all stem, leaf and branch traits varied among species, grown both in monocultures and in mixtures.

2.3.1 Stem size

Mean basal area increased from $2.5 \pm 4.0\,cm^2$ in early spring 2011 to $9.7 \pm 4.3\,cm^2$ in late summer 2012. In all four assessments, from early spring 2011 to late summer 2012, tree basal area varied among species grown in monocultures ($p<0.01$, Table 2.3) and in mixtures ($p<0.001$, Table 2.3). In spring 2011 the species with the largest mean basal area were *Choerospondias axillaris* (10.97 ± 6.97 cm^2), *Triadica sebifera* (3.50 ± 3.13 cm^2) and *Nyssa sinensis* (3.50 ± 2.30 cm^2); in summer 2012, *C. axillaris* (31.82 ± 22.19 cm^2), *N. sinensis* (20.46 ± 14.37 cm^2) and *Schima superba* (15.62 ± 11.88 cm^2).

In spring 2011, richness did not affect basal area (Table 2.3). We observed a gradual increase of basal area with increasing species richness in summer 2011 and spring 2012 ($p<0.1$, Table 2.3), with a significant increase in basal area with increasing species richness in summer 2012 ($p<0.01$, Table 2.3, Fig. 2.1).

2.3.2 Leaf production

Total number of leaves

At the end of the growing season, in summer 2011 and 2012, the total number of leaves varied among species grown in monocultures (summer 2011: $F_{12,19.2}=3.08$, $P<0.05$; summer 2012: $F_{12,21.4}=3.81$, $P<0.01$) and in mixtures (summer 2011: $F_{14,288.2}=14.14$, $P<0.001$; summer 2012: $F_{14,316.7}=22.45$, $P<0.001$). Species richness did not affect the total number of leaves in any year during this study (summer 2011: $F_{1,19.5}=0.07$, $P>0.7$; summer 2012:

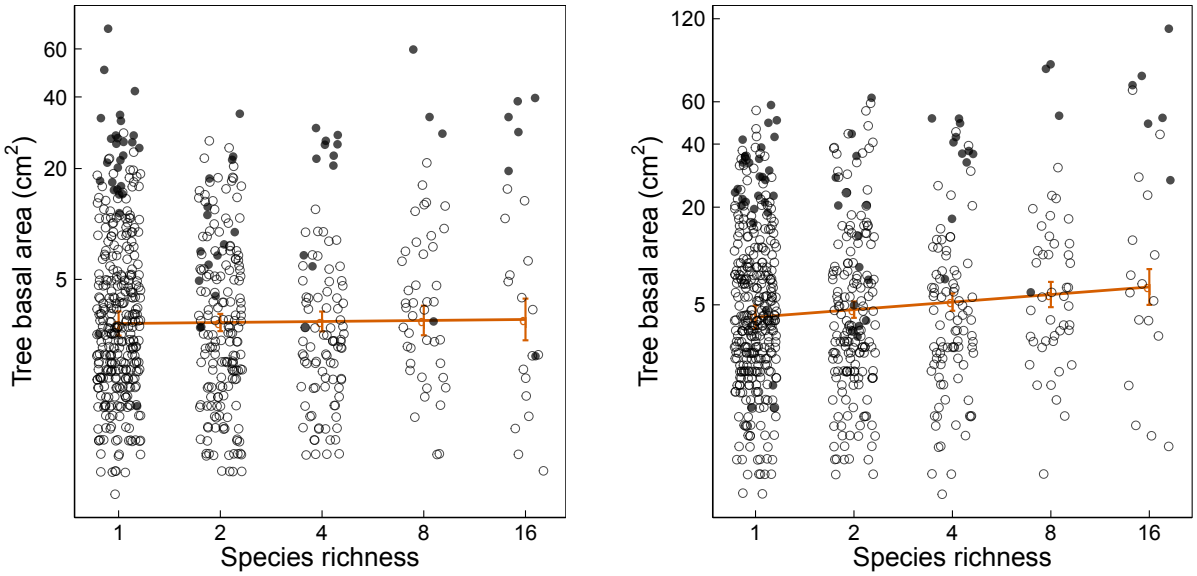


Figure 2.1: Tree basal area in summer 2011 (left) and summer 2012 (right) as function of tree species richness. Tree basal area significantly increased with richness in 2012. Closed circles indicate values for *C. axillaris* individuals; open circles, values for all others. Line shows predicted values of the statistical models (see methods). Error bars are standard errors.

$F_{1,21.6}$=2.75, P>0.10). However, the interaction species identity and species richness was significant for the total number of leaves in summer 2012 ($F_{14,236.1}$=1.85, P<0.05).

Leaf emergence rate

Leaf emergence varied among species grown in monocultures ($F_{12,14.7}$=4.34, P<0.01) and in mixtures ($F_{14,89.1}$=2.88, P<0.01) during the summer of 2011. The highest mean leaf emergence rate was measured for the species *Quercus fabri*, *T. sebifera* and *Liquidambar formosana*; the species with the lowest measured mean leaf emergence rate were *C. axillaris*, *Koelreuteria bipinnata* and *Rhus chinensis*. Species richness had no observed effect on leaf emergence ($F_{1,15.5}$=3.10, P=0.099).

Leaf emergence rate did not show an effect of species richness from April 2012 to May 2013 ($F_{1,55.3}$=0.06, P>0.05; Fig. 2.2) but the rate of leaf emergence varied among species grown in monocultures ($F_{14,10}$=2.78, P=0.054) and in mixtures ($F_{14,3.9}$=5.31, P<0.01). *S. superba*, *Castanopsis sclerophylla* and *T. sebifera* showed the greatest mean leaf emergence; species with the lowest mean leaf emergence rate were *Sapindus mukorossi*, *R. chinensis* and *C. axillaris*. Emergence rate decreased throughout the growing season (linear date: $F_{1,232.4}$=80.72, P<0.001; time as factor: ($F_{5,220.9}$=10.96, P<0.001).

Leaf mortality

In the summer of 2011, leaf mortality varied among species grown in monocultures ($F_{12,21.7}$=3.0, P<0.05) and in mixtures ($F_{14,146.8}$=2.8, P<0.01). The highest mortality

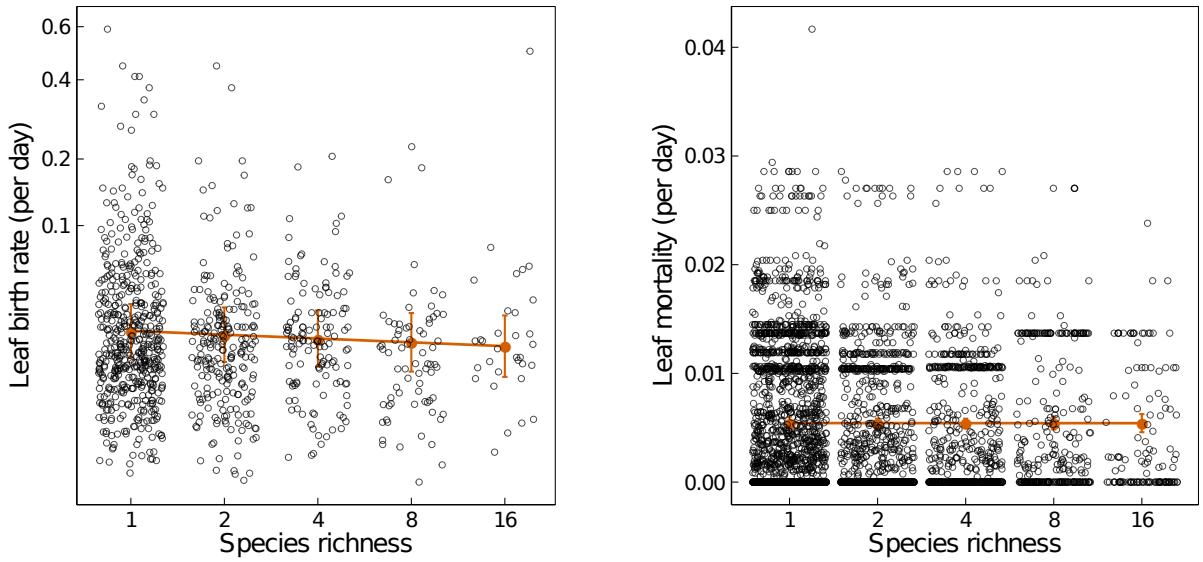


Figure 2.2: Leaf emergence (left) and mortality (right) rate in 2012 as function of tree species richness. Leaf emergence and mortality rates did not vary with species richness. Open circles indicate values of leaf emergence in summer or leaf mortality from spring 2012 to the next year. Line shows predicted values of the statistical models (see methods). Error bars are standard errors.

was observed on average in the species *T. sebifera*, *C. sclerophylla* and *S. superba*; the lowest observed mean mortality corresponded to *S. mukorossi*, *Q. fabri* and *Quercus serrata*. Species richness did not affect leaf mortality ($F_{1,13.7}$=2.4, P=0.14).

From April 2012 to May 2013, leaf mortality was not affected by species richness ($F_{1,81.2}$=0.8, P=0.37, Fig. 2.2) but this varied among species grown in monocultures ($F_{14,36.3}$=3.7, P<0.001) and grown in mixtures ($F_{14,75.7}$=8.1, P<0.001). The rate of mortality was greatest for *T. sebifera*, *R. chinensis* and *K. bipinnata*; *Cyclobalanopsis glauca*, *Lithocarpus glaber* and *Cyclobalanopsis myrsinifolia* showed the lowest rate. Mortality increased with the age of the cohort ($F_{1,3563.4}$=719.7, P<0.001) and the census date ($F_{1,1778.1}$=356.1, P<0.001). In the second model, when cohort and census date were fitted before richness, species richness did not have an effect on mortality ($F_{1,84.6}$=0.7, P>0.05).

Leaf size

Leaf length varied among species, both in monocultures ($F_{12,3.2}$=21.9, P<0.05) and in mixtures ($F_{14,31.4}$=91.0, P<0.001) in summer 2011. Leaf length did not show an effect of species richness ($F_{1,4.2}$=3.6, P=0.13).

Leaf length varied among species grown in monocultures ($F_{14,33.5}$=33.9, P<0.001) and in mixtures ($F_{14,61.8}$=64,2, P<0.001) in summer 2012. Furthermore, the leaves of trees grown in monocultures were longer on average than those of trees grown in mixtures ($F_{1,30.9}$=4.3, P<0.05). Leaf length increased with increasing richness ($F_{1,14.1}$=8.5, P<0.05, Fig. 2.3).

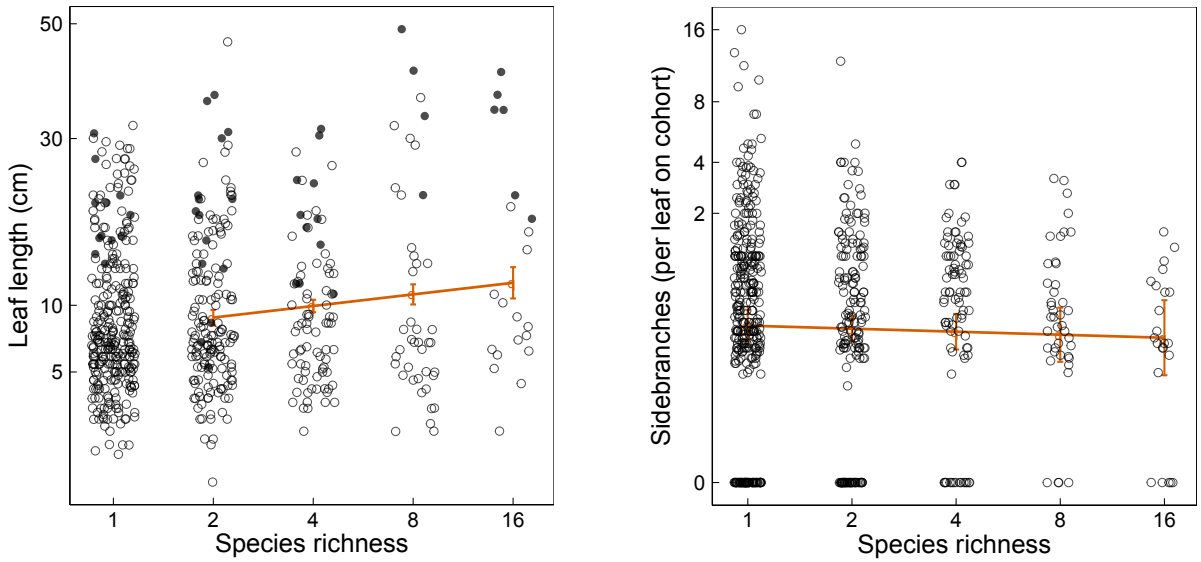


Figure 2.3: Leaf length (left) and branching rate (right) in summer 2012 as function of tree species richness. Leaf length significantly increased with species richness; branching rate was not affected by species richness. Closed circles indicate values for *C. axillaris* individuals; grey circles, values for all other species. Line shows predicted values of the statistical models (see methods). Error bars are standard errors.

2.3.3 Branching pattern

Branching rate

In summer 2012, branching rate (i.e. number of emerged branches per cohort leaf) varied among species grown in monocultures ($F_{14,30.9}$=8.36, P<0.001) and in mixtures ($F_{14,307.7}$=13.97, P<0.001). Branching rate did not show an effect of species richness ($F_{1,29.7}$=0.01, P>0.05, Fig. 2.3). The interaction of species identity and species richness grown in mixtures showed a significant effect on branching rate ($F_{14,324.1}$=1.87, P<0.01).

2.4 Discussion

In an earlier study, we found a positive relationship between species richness and stand wood productivity in the BEF-China experimental site (Chapter 1). To explore the effect of species richness on the leaf fraction, we tested the effect of species richness on leaf production, leaf size and branching patterns. We found that towards the end of our study period (summer 2012), trees growing in more diverse stands had a larger basal area and larger leaves. Contrary to our expectations, leaf production and branching rate did not respond to species richness.

The gradual emergence of a richness effect on tree basal area confirms the results of our previous study at stand level (Chapter 1). Using a larger number of plots from our experiment (386 plots vs. 62 plots here) in 2012 we found that the increase of stand productivity in more diverse plots was due to tree growth and not differential rates of mortality or re-

cruitment among the diversity levels. Furthermore, variability in stand productivity was explained by the presence of *Choerospondias axillaris* and *Schima superba* trees in the plots. Specifically, the biodiversity-stand productivity relationship was negative in plots with *S. superba*, but in plots with *C. axillaris* this relationship went from negative (in 2011) to positive (in 2012). In this study we found that both species were characterized by their large mean tree size, which we anticipated as both species are typical of early successional communities and their growth is enhanced by rich light conditions (Pakkad *et al.*, 2003; Guchou *et al.*, 2007). Interestingly, only *C. axillaris*, a species with a high phenotypic plasticity in growth-related traits (Böhnke & Bruelheide, 2013), showed an increase in individual basal area with richness in 2012. The negative relationship between species richness and stand productivity in plots with *S. superba* (Chapter 1) could therefore be explained by the higher relative abundance and resulting higher summed basal area of *S. superba* in low diversity plots. Our results support successional theory which predicts that during stand initiation, stands containing only early successional fast-growing species will be more productive than stands of early and late successional species mixtures. We hypothesize that in plots with *C. axillaris* intraspecific competition was so great in monocultures that individual growth was supressed. In contrast, individuals grown in mixtures benefited from reduced intraspecific competition. This hypothesis is supported by the observed reduction in tree growth with increasing size of the neighboring trees at our study site (Li *et al.*, 2014).

Furthermore, the diversity effect on leaf length was particularly observed for individuals of *C. axillaris*, which has compound leaves. In early successional vegetation, when rapid vertical growth is preferred, to build short-lived compound leaves can be more cost-effective than to construct woody side branches. Species with strong apical dominance such as *C. axillaris* may use their compound leaves as low-cost disposable 'branches' to cover a large area in the canopy space (Givnish, 2010). A recent terrestrial laser scanning study at our study site in 2011 showed that growth of *C. axillaris* individuals was more vertical in monocultures and more lateral in mixtures (Li, pers. comm).

The invariable leaf production along our richness gradient was unexpected because wood production, at individual or stand level (Chapter 1) increased with species richness. However, a subsequent study in the same plots found that leaf area at stand level (LAI) did not vary with richness in summer of 2013 (Peng, 2014). Similarly, the lack of response of branching rates to species richness corresponds to the reduced intraspecific variability in vertical leaf area distribution and crown architecture of trees in a nearby subtropical mixed forest (Guisasola *et al.*, 2015).

Our data suggests that the effect of species richness on tree size is not related to increments in leaf production but rather to changes in leaf morphology. Indeed, morphological and physiological factors play a important role in determining tree growth and its capacity to adapt to environmental changes. A recent review by Poorter *et al.* (2012) concluded that plants are more able to respond to environmental changes by adjusting their leaf morphology (SLA) than by adjusting their biomass allocation patterns to leaves. Similarly, in a Chinese subtropical mixed forest two-old year saplings adjusted to low light conditions by increasing their SLA and net assimilation rate, whereas the leaf mass ratio

remained constant (Li, 2011). Processes other than photosynthesis may however control plant growth, e.g. nitrogen availability (Norby *et al.*, 2010; Norby & Zak, 2011; Palacio *et al.*, 2014; Körner, 2015). Indeed, a 10-year old biodiversity experiment recently showed that litter-mediated interactions among trees contribute more to overyielding than light partitioning (Sapijanskas *et al.*, 2013).

Overall, our study demonstrates that tree species richness enhances stem growth but not leaf production during stand development. At this stage of stand initiation the diversity-growth relation is mainly driven by a fast-growing species, *C. axillaris*, which suggests the predominance of selection effects (Loreau & Hector, 2001). In addition, the disproportionate response of leaf and wood production suggests that the complementary use of the canopy space through light partitioning is not a (main) driver of increased productivity at higher species richness.

Last, our results suggests that young plantations can storage more carbon if they are managed for diversity. This is relevant for forestry policies in China, where national reforestation and afforestation programs have focused on species-poor plantations.

Table 2.3: Results of mixed-effects model analysis for tree basal area in spring and summer of 2011 and 2012. numDf: degrees of freedom of term, denDf: degrees of freedom of error term (which can be fractional in REML analysis), F statistic, P.

	Spring 2011				Summer 2011				Spring 2012				Summer 2012			
	numDf	denDf	F	P	numDf	denDf	F	P	numDf	denDf	F	P	numDf	denDf	F	P
Fixed terms																
Is.mono	1	11.5	0.81	0.388	1	32.7	0.83	0.369	1	21.3	0.01	0.943	1	33.4	0	0.994
Monospecies	13	8.4	9.99	<0.001	14	35.2	8.44	<0.001	12	24.1	6.63	<0.001	14	41.8	5.32	<0.001
log(diversity)	1	17.4	0.53	0.477	1	25.5	3.27	0.082	1	9.2	3.87	0.080	1	14.5	10.57	0.006
Mixspecies	13	13.3	18.64	<0.001	14	49.6	21.7	<0.001	14	31.3	12.33	<0.001	14	59.5	17.29	<0.001
log(diversity):mixspecies	13	23.2	0.53	0.885	14	87.5	1.27	0.240	14	51.3	1.24	0.278	14	82.2	1.44	0.156
Random terms	VC	s.e.			VC	s.e.			VC	s.e.			VC	s.e.		
composition:plot	0.003	0.006														
plot	0.009	0.006			0.022	0.009			0.013	0.013			0.017	0.015		
plot:mixsp	0.005	0.005			0.005	0.006			0.018	0.014			0.027	0.014		
residual	0.051	0.003			0.074	0.004			0.077	0.005			0.101	0.006		

3 Tree diversity enhances stand productivity but not leaf area in subtropical forest

Nadia Castro Izaguirre, Xiulian Chi, Zhiyao Tang, Martin Baruffol, Bernhard Schmid and Pascal A. Niklaus

Abstract

Several studies have shown that wood production increases with tree diversity. However, little is known about the effect of tree diversity on leaf production. As resource-capturing organs, leaves can influence stand productivity. Thus, integrative studies of wood and leaf fraction are necessary to understand the mechanisms underlying the biodiversity-productivity relationship in forests.

Here we studied stand basal area, vertical structure, leaf area, and their relationship with tree species richness in a subtropical forest in China. We hypothesized that more diverse stands achieve higher aboveground productivity through a more complete utilization of the canopy vertical space and higher stand leaf area. We estimated stand basal area and its increase over four years, stand leaf area, and variability in tree heights as measure of vertical space use in 25 plots, which cover a gradient of successional age and tree species richness. In addition, we tested for richness effects on aboveground carbon stocks derived using allometric relations.

We found that more diverse stands were characterized by significantly more variable tree height, higher stand basal area and annual stand basal area increases, and estimated plot aboveground C stocks. In contrast, LAI did not respond to species richness.

Overall, our study demonstrates that tree species richness enhances stand productivity but not leaf area during secondary succession. Thus, our results suggest that the complementary use of the canopy space through light partitioning is not a (main) driver of increased productivity at higher species richness.

3.1 Introduction

A positive relationship between diversity and woody production has been observed in natural forests worldwide, from boreal to tropical biomes (Vilà *et al.*, 2007; Paquette & Messier, 2011; Gamfeldt *et al.*, 2013; Baruffol *et al.*, 2013; Lasky *et al.*, 2014). Little is known, however, about the effect of diversity on leaf biomass. While wood production is probably the most visible component of productivity in a forest, leaves are functionally important because they intercept light, assimilate carbon through photosynthesis and consequently influence stand productivity. Thus, an integrative study of the effects of tree richness on wood and leaf components would help to clarify the underlying mechanisms in the biodiversity-productivity relationship.

Stand leaf area is a key characteristic of forest canopy structure. Recently, Morin *et al.* (2011) postulated that if increasing species richness leads to a higher diversity in shade tolerance, maximal heights and growth ability, more diverse stands that contain shade-tolerante and light demanding species can fill more light niches and develop a multilayer canopy. As a result of this vertical stratification, leaf area would increase and stand productivity rise due to enhanced light capture and photosynthesis. Although the complementary use of the canopy space through light partitioning is often proposed as a mechanism driving the positive diversity-productivity relationship (e.g. Potvin & Gotelli, 2008; Jucker *et al.*, 2014b; Ruiz-Benito *et al.*, 2014; Ewel *et al.*, 2015; Zhang & Chen, 2015), only a few studies have empirically tested the effect of species richness on canopy structure.

In temperate broad-leaved forests neither canopy space filling (Seidel *et al.*, 2013) nor LAI (Jacob *et al.*, 2010) were affected by tree species richness. In contrast, canopy packing was more efficient in more diverse stands across Europe (Jucker *et al.*, 2015). However, those forests showed a negative (Jacob *et al.*, 2010) or no dependency (Seidel *et al.*, 2013; Jucker *et al.*, 2015) of productivity on species richness. Furthermore, they are characterized by their low diversity (up to 3–5 species). Thus, the relationship between species richness, stand leaf area and productivity is still an open question in species-rich stands that show an increase of productivity with species richness.

Recently, we found that stand basal area and its increment increase with species richness in a highly diverse mixed broad-leaved forest in subtropical China (Baruffol *et al.*, 2013). By systematically selecting plots that represent different levels of tree species richness and stand successional age (i.e. time elapsed since the last logging event), our study had more power to detect causal relationships than conventional sample surveys. Here, we explore the mechanisms underlying the positive diversity-productivity relationship by simultaneously analyzing the effects on diversity on aboveground biomass, vertical structure and stand leaf area in the same plots. We hypothesize that more diverse stands achieve higher aboveground productivity through a more complete utilization of the canopy vertical space and higher stand leaf area. We estimated the stand basal area and its increase over four years, stand leaf area, and variability in tree heights as measure of vertical space use in the same study plots. Given the importance of forests in global carbon cycling and climate regulation, we also tested for species richness effects on aboveground carbon

stocks derived using allometric relations.

3.2 Methods

3.2.1 Study site and experimental design

We studied the effect of tree species richness and stand successional age on the canopy vertical structure, leaf area index (LAI) and stand basal area and its 4-year increment, and stand aboveground biomass carbon stock in a comparative study in Gutianshan National Nature Forest Reserve, Zhejian province, south-east China (29°15'N, 118°07'E). The climate is subtropical monsoon, with a mean annual air temperature of 15.1 °C and a mean annual precipitation of 2000 mm. The vegetation is typical of mixed broad-leaved forests. A total of 1462 seed plant species belonging to 684 genera and 149 families are found in the 81 km^2 reserve, with 258 of these species being woody. The number of evergreen and deciduous species is similar but the former dominate by number of individuals. The reserve covers a mosaic of forest patches in different successional stages, from five to more that 80 years since the last logging event (see Bruelheide *et al.*, 2011, and references therein). In 2008, 27 plots were established to cover a gradient of species richness and successional age (Bruelheide *et al.*, 2011). The size of each plot was 30 m × 30 m and the average distance between them was ca. 3 km (minimum distance: 40 m). Successional stand age was determined based on the age of the fifth-largest tree of each plot (determined from a stem core) and assigned to one of five age classes (<20, 20–40, 40–60, 60–80, >80 years old with 3-7 plots per age class) (Baruffol *et al.*, 2013). Two plots were lost in the course of the study due to illegal logging, so that the present study bases on inventory data from 25 plots.

3.2.2 Tree inventory

In summer of 2008 and 2012 we measured the diameter at breast height (DBH) of all trees with a DBH $\geq$ 10cm. In addition, in 2012 we measured their height (and length if the tree was leaning) with a hypsometer (Vertex III, Haglöf AB, Sweden). Stand basal area (SBA) was estimated as the sum of the total basal area of the individual trees ($m^2\,ha^{-1}$). Stand basal area increment (ΔSBA) was calculated as the increase of stand basal area of all surviving trees from the first census to the second ($m^2\,ha^{-1}\,yr^{-1}$).

As a proxy of stand vertical structure, we used the standard deviation of tree height (SD_{height}). This parameter, relatively easy and fast to asses in the field, can be used as a proxy of the vertical layering of the foliage (McElhinny *et al.*, 2005).

3.2.3 Stand leaf area

Because our study site is a mixed broad-leaved forest, LAI was assessed by hemispherical photography in early spring and late summer of 2012. The timing of the assessments was chosen to capture either the canopy when only evergreen leaves were present or when both evergreen and deciduous leaves were present, respectively.

Plots were divided into nine quadrats and at the center of each quadrat, we took hemispherical photographs of the canopy at 1.5 m above ground using a digital camera (Nikon D3000) with a fish-eye lens (Sigma 4.5 mm f/2.8). The camera, mounted on a tripod equipped with a bubble level, was oriented so that the top of the photographs was aligned with the geographic north. Photos were acquired vertically upwards and, to minimize glare from direct sunlight, taken either under overcast sky conditions, before sunrise or after sunset. The exposure was set manually to f/5.6 and ISO 200. Four photographs were taken, the first at the automatic exposure read by the camera, and the three others underexposed by 1, 2 or 3 stops by varying the shutter speed. For each point, we selected the picture with the highest exposure but without noticeable blooming effect (Schleppi *et al.*, 2007; Thimonier *et al.*, 2010). Photographs were then preprocessed to discriminate between vegetation and open sky, using a custom software that allowed to adjust for uneven sky illumination by defining light intensity thresholds for selected polygons that then were extrapolated based on delauney triangulation (P. Niklaus, unpublished). Correct discrimination was carefully visually done in all images, and leaf area estimated using the Hemisfer software (Schleppi *et al.*, 2007; Thimonier *et al.*, 2010), using a total observed zenith angle of 75° divided into five rings of 15°. Plot-level LAI was calculated as the average of LAI estimated from the nine quadrats in spring (LAI_{spring}) and summer (LAI_{summer}).

3.2.4 Stand aboveground carbon stocks

To estimate total aboveground biomass (stem, branches, and leaves) we used allometric equations that were developed from in and around our study area (Lin *et al.*, 2012). If a tree had multiple stems, we calculated the biomass for each stem. To convert biomass ($Mg\,ha^{-1}$) to carbon stock (C stock, $Mg\,C\,ha^{-1}$) we used a ratio of 0.5.

3.2.5 Species richness, functional and phylogenetic diversity

Species richness was defined as the number of tree species in each plot. Functional and phylogenetic diversity were calculated following Baruffol *et al.* (2013). We selected a set of growth-related species traits to calculate functional diversity sensu Petchey & Gaston (2006): leaf seasonality (evergreen vs. deciduous), leaf habit (broadleaved vs. coniferous), specific leaf area (SLA), leaf carbon to nitrogen ration (C:N), leaf size (dry weight of a typical mature leaf), the typical maximum height reached by mature individuals, and the stem wood density. Maximum height was obtained from published literature (Editorial Committee for Flora Reipublicae Popularis Sinicae, 2004), while all other traits were collected from individuals sampled in Gutianshan National Nature reserve (Böhnke *et al.*, 2012; Kröber *et al.*, 2012). For three species wood density was taken from the global wood density database (Chave *et al.*, 2009), after re-scaling the values based on the correlation of wood densities of species present in both datasets. All traits were normalized to zero mean and unit variance; all missing values were set to zero. We generated trait dendograms for these traits, and calculated the total branch length of species occurring in a plot (euclidean distances, complete linkage agglomeration).

Using a phylogenetic tree including 440 woody species present in our study site (Baruffol *et al.*, 2013, and see methods therein) we calculated PD as the total branch length defined by the subset of species occurring in a plot.

3.2.6 Statistical analysis

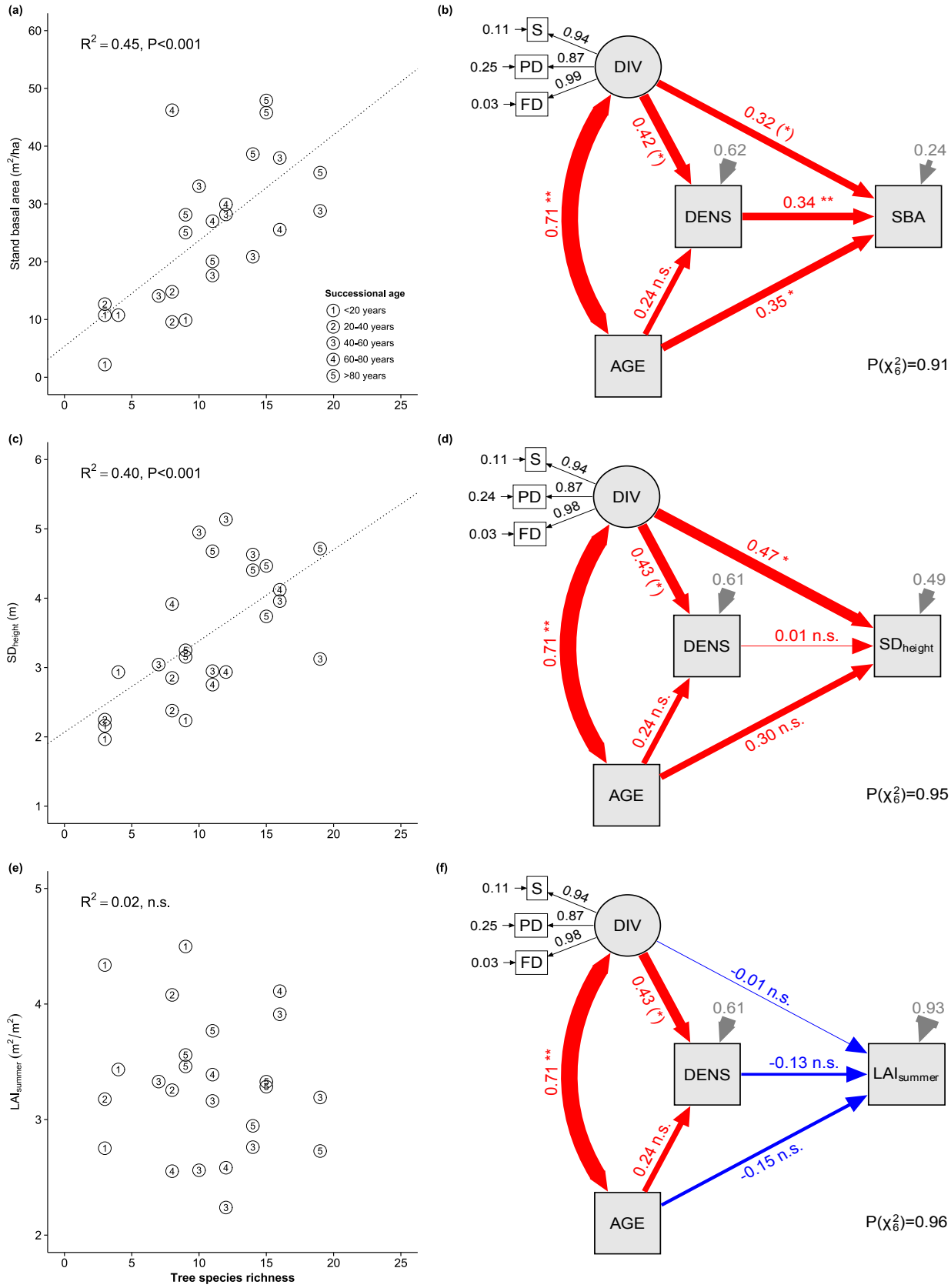
To test for the effects of species richness and stand successional age on stand basal area, ΔSBA, SD_{height}, LAI_{spring} and LAI_{summer}, and C stock , we fitted multiple regressions with sequential sum of squares (lm function of R). Because richness and stand successional age are correlated, we tested the influence of richness after adjusting for age (richness fitted after age) and the influence of age after adjusting for richness (age fitted after richness). Next, we used structural equation models to explore the relations among tree diversity (latent variable defined by species richness, functional diversity, and phylogenetic diversity), stand successional age, and their indirect effects mediated by changes in tree density (i.e. the number of trees per plot).

3.3 Results

In 2012 mean stand basal area was 24.83 $m^2\,ha^{-1}$ (range 2.20–47.91), mean LAI_{spring} 2.83 (range 1.26–3.5), mean LAI_{summer} 3.3 (range 2.24–4.5), and mean C stock 63.42 $Mg^2\,ha^{-1}$ (range 4.48–134.7). The number of trees that were alive in 2008 and 2012 in each plot (tree density) was on average 60 (range 10–96); the mean number of species was 11 (range 3–19).

3.3.1 Stand basal area

Stand basal area and ΔSBA increased linearly with species richness (SBA: $F_{1,22}=28.49$, $P<0.001$; ΔSBA: $F_{1,22}=11.36$, $P<0.01$ in multiple regression with sequential sum of squares for species richness fitted before stand age; Fig. 3.1, Fig. S1). Although stand age and species richness are partially confounded, the effect of richness remained (partially) significant after adjusting for successional age (SBA: $F_{1,22}=4.06$, $P<0.1$; ΔSBA: $F_{1,22}=14.14$, $P<0.01$ for richness fitted after successional age). Structural equation models revealed that the effect of diversity on stand basal area and ΔSBA was mediate by an increase in tree density (path coefficients linking DIV-DEN with SBA and ΔSBA, respectively; Fig. 3.1, Fig. S1) and in individual size and growth (path coeffecients linking DIV with SBA and ΔSBA, respectively). The direct effect of diversity was particularly strong on ΔSBA. Succesionally older stands had a higher stand basal area (path AGE-SBA) but a lower ΔSBA (path AGE-ΔSBA). In both cases, the effect was not mediated by a change in tree density (path AGE-DENS-SBA and path AGE-DENS-ΔSBA) but by a change in individual size and growth (path DENS-SBA and path DENS-ΔSBA).


(a)
R² = 0.45, P<0.001
Stand basal area (m²/ha)
Successional age
1 <20 years
2 20-40 years
3 40-60 years
4 60-80 years
5 >80 years
(b)
0.11 S
0.25 PD
0.03 FD
0.94
0.87
0.99
DIV
0.32 (*)
0.42 (*)
0.62
0.24
DENS
SBA
0.34 **
0.71 **
0.24 n.s.
0.35 *
AGE
P(χ²6)=0.91
(c)
R² = 0.40, P<0.001
SDheight (m)
(d)
0.11 S
0.24 PD
0.03 FD
0.94
0.87
0.98
DIV
0.47 *
0.43 (*)
0.61
0.49
DENS
SDheight
0.01 n.s.
0.71 **
0.24 n.s.
0.30 n.s.
AGE
P(χ²6)=0.95
(e)
R² = 0.02, n.s.
LAIsummer (m²/m²)
Tree species richness
(f)
0.11 S
0.25 PD
0.03 FD
0.94
0.87
0.98
DIV
-0.01 n.s.
0.43 (*)
0.61
0.93
DENS
LAIsummer
-0.13 n.s.
0.71 **
0.24 n.s.
-0.15 n.s.
AGE
P(χ²6)=0.96

3.3.2 Stand vertical structure

As species richness increased, SD_{height} increased ($F_{1,22}$=16.97, P<0.001 when richness fitted before stand age; $F_{1,22}$=4.55, P<0.05 when richness fitted after age; Fig. 3.1). The effect of diversity was not mediated by any change in tree abundance (path DIV-DENS-SD_{height}) but it was only direct (path DIV-SD_{height}, Fig. 3.1). Stand age had no effect, direct or indirect, on SD_{height}.

3.3.3 Leaf area index

Species richness had no effect on LAI_{spring} (P=0.6) or LAI_{summer}(P=0.5 for richness fitted before age; Fig. 3.1). In both cases, the effect of richness remained insignificant after adjusting for successional age (LAI_{spring}: P=0.4; LAI_{summer}: P= 0.9). Similarly, the structural equation model showed that LAI, either in spring or summer, was not affected by diversity, stand age or tree density (Fig. 3.1).

3.3.4 Carbon stock

Similarly to SBA, a positive effect of species richness was also evident when considering the carbon stock in the aboveground biomass ($F_{1,22}$=21.82, P<0.00 when richness fitted before age; $F_{1,22}$=4.16, P=0.054 when richness fitted after age; Fig. 3.2). The effect of diversity was mediated by an increase in tree density (path DIV-DENS-C stock, Fig. 3.2) and in individual C stock (path DIV-C stock). In contrast to stand basal area, stand age did not influence the C stock (path AGE-C stock).

3.4 Discussion

We tested whether species richness affected productivity of leaves and stems (LAI and stand basal area), and vertical canopy space use. Our rationale was that the main mechanism for the positive relation between richness and productivity is the complementary use of the canopy space, possibly through light partitioning. More diverse stands were charac-

Figure 3.1 ***(preceding page)*:** Left: Stand basal area (a), vertical structure (c) and leaf area (e) as a function of tree species richness and stand successional age. Right: Results of structural equation modeling (SEM) analysis for stand basal area (b), vertical structure (d) and leaf area (f) in dependence of successional age, tree diversity, and tree stem density. Species richness enhanced woody production (SBA) and vertical structure but did not affect stand leaf area. Path diagrams indicate effects of tree species diversity on the two dependent variables, either directly or indirectly via increases in tree density. The diagrams show standardized path coefficients (red: positive; blue: negative) and associated statistical significances (*** P<0.001; ** P<0.01; *P<0.05; (*) P<0.1). Variable abbreviations: S = species richness, PD = phylogenetic diversity, FD = functional diversity, DIV = diversity (latent variable related to previous three), AGE = successional age, DENS = tree density, SBA = total stem basal area, SD_{height} = height variation, LAI_{summer} = LAI in summer.

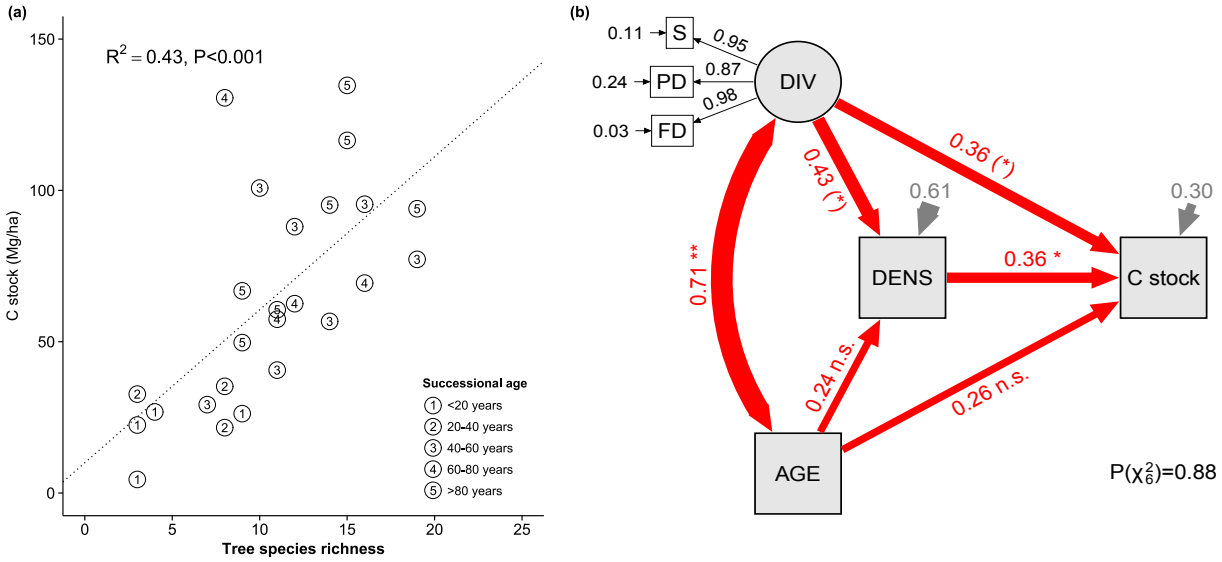


Figure 3.2: Left: C stock in the aboveground biomass (a) as function of tree species richness and stand successional age. Line shows predicted values of the statistical models (see methods). Right: Results of structural equation modeling (SEM) analysis for C stock (b) in dependence of successional age, tree diversity, and tree stem density. C stock increased with tree species richness. Path diagrams indicate effects of tree species diversity on the two dependent variables, either directly or indirectly via increases in tree density. The diagrams show standardized path coefficients (red: positive; blue: negative) and associated statistical significances (*** P<0.001; ** P<0.01; *P<0.05; (*) P<0.1). Variable abbreviations: S = species richness, PD = phylogenetic diversity, FD = functional diversity, DIV = diversity (latent variable related to previous three), AGE = successional age, DENS = tree density, C stock = C stored in the aboveground biomass.

terized by more variable tree height, higher stand basal area and annual stand basal area increases, and estimated plot aboveground C stocks. Interestingly, LAI did not respond to species richness, indicating that aboveground biomass increases were not mediated by leaf area changes.

The effect of diversity on stand basal area and its 2008–2012 increase was driven by an increase in tree density and individual size. In comparison to our previous 2-year study (Baruffol *et al.*, 2013), the effect of diversity on ΔSBA was larger and more significant (path coefficients 0.74 (p <0.01) vs. 0.58 (p<0.05) in 2008-2012 and 2008-2010, respectively). Thus, our results indicate persistent effects of species richness on stem growth.

Leaf area, in contrast, did not react to changes in diversity. Because leaf area is related to photosynthesis and therefore, to productivity, the lack of response was surprising. Likewise, the behavior of leaf area was uncoupled from height variability (i.e. vertical stratification), which increased in more diverse stands and suggested a better use of the canopy space through complementarity. However, a recent study in forest stands across Europe showed that crown morphology, i.e. intraspecific variation in crown morphology, is more important than vertical stratification to explain the increase of canopy use efficiency

with diversity (Jucker *et al.*, 2015). In our study area tree species show a high plasticity in responses to forage for light. As saplings, they can adjust their SLA to light conditions (Böhnke & Bruelheide, 2013), whereas as adults competition in the local neighborhood influences their stem inclination and crown displacement (Lang *et al.*, 2010). Thus, an increase in crown sizes might compensate for a low vertical stratification, so that all stands, either with low or high species richness, achieve a similar leaf area.

Despite equal leaf area, more diverse stands had higher woody biomass and grew faster. One reason maybe more efficient light use. For example, low available light in the lower canopy could be better exploited in a more diverse stand, where shade-tolerant species are more likely to be present. Similarly, even if two stands have the same LAI, structural differences (e.g. clumping of trees that leads to shading among crowns) or the leaf area arrangement can alter light absorption (Binkley *et al.*, 2013), or light use efficiency (Hardiman *et al.*, 2011, 2013). On the other hand, processes other than photosynthesis might control plant growth, e.g. nitrogen availability (Norby *et al.*, 2010; Norby & Zak, 2011; Palacio *et al.*, 2014; Körner, 2015). Indeed, a 10-year old biodiversity experiment recently showed that litter-mediated interactions among trees contribute more to overyielding than light partitioning (Sapijanskas *et al.*, 2013).

Our forest stands stored 4.5–135 Mg C ha^{-1} in aboveground biomass (i.e. stem, branches and leaves), which is within the range reported for subtropical evergreen broad-leaved forests of China (Lin *et al.*, 2012). Carbon storage, however, varied with species richness, even after first correcting for stand age. Structural equation modelling even suggested that diversity was a more important determinant of carbon stocks than successional age in our study. Carbon stock increased by 50.6 Mg C ha^{-1} per 10 extra species, or by +83% when doubling species number from 10 to 20. Biodiversity effect sizes (Zr of 0.42–0.88 depending whether species richness was fitted before or after successional age) are larger that what has been found in recent meta-analyses of grassland biodiversity experiments (Balvanera *et al.*, 2006) and forest plantation data (Piotto, 2008). While other studies have indicated that the diversity-carbon storage relationship is asymptotic in forests (Zhang *et al.*, 2012; Vilà *et al.*, 2013; Ruiz-Benito *et al.*, 2014), the linear relationship found in our study suggests that functional redundancy and niche overlap do not substantially reduce effects of additional species even in our species-rich system (Loreau *et al.*, 2001; Hooper *et al.*, 2005).

Forests can store large amounts of carbon in belowground biomass . We do not have root biomass data, but believe that the potential effects of species richness on root biomass will not substantially alter the effects we found on total biomass carbon. First, more biomass is generally allocated aboveground than belowground; for Chinese forests (Wang *et al.*, 2014) and the world's subtropical forest (Mokany *et al.*, 2006) a root to shoot ratio of 0.23 has been reported. Second, allometric considerations suggest that a higher stand basal area not only corresponds to larger aboveground but also to increased beloweground biomass. Indeed, root biomass increments with species richness have been observed in temperate and boreal forests (Meinen *et al.*, 2009; Brassard *et al.*, 2011).

Our findings are relevant for forestry policies in China, where C storage and sequestration have increased in the past three decades (Fang *et al.*, 2001; Shi *et al.*, 2011) and

forest is expected to continue to act as a carbon sink at least until 2050 (Xu *et al.*, 2010). This increase has been attributed to national reforestation and afforestation programs (Xu *et al.*, 2010; Shi *et al.*, 2011), which are currently concentrated on monocultures. Thus, we consider that managing for forest diversity will be an important mitigation effort to effectively increase C storage.

Overall, our study demonstrates that tree species richness enhances stand productivity but not leaf area during secondary succession. The disproportionate response of leaf area and woody biomass suggests that the complementary use of the canopy space through light partitioning is not a (main) driver of increased productivity at higher species richness. Our results suggest that this mechanisms may be less important in the investigated ecosystem than in others (Jucker *et al.*, 2014b, 2015) and that the availability of resources other than light might control stand growth.

3.5 Appendix

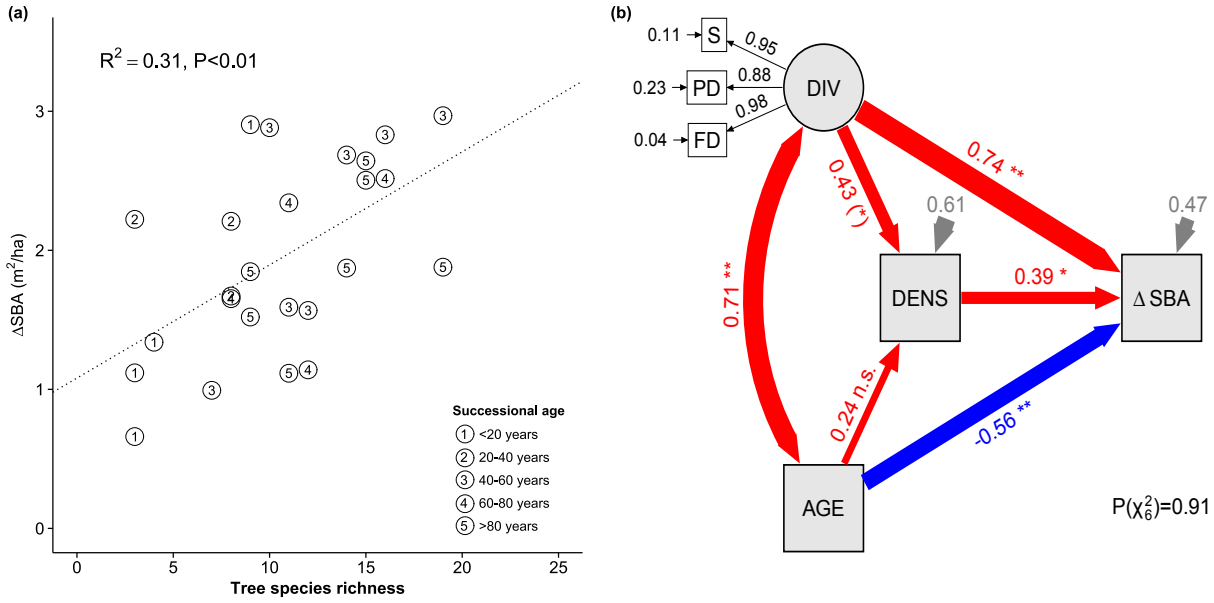


Figure S1: Left: ΔSBA (a) as function of tree species richness and stand successional age. Line shows predicted values of the statistical models (see methods). Right: Results of structural equation modeling (SEM) analysis for ΔSBA (b) in dependence of successional age, tree diversity, and tree stem density. ΔSBA increased with tree species richness and decreased with stand age. Path diagrams indicate effects of tree species diversity on the two dependent variables, either directly or indirectly via increases in tree density. The diagrams show standardized path coefficients (red: positive; blue: negative) and associated statistical significances (*** P<0.001; ** P<0.01; *P<0.05; (*) P<0.1). Variable abbreviations: S = species richness, PD = phylogenetic diversity, FD = functional diversity, DIV = diversity (latent variable related to previous three), AGE = successional age, DENS = tree density, ΔSBA = 2008-2012 increase of stand basal area.

General discussion

In this thesis, I examine the effect of tree species richness on primary productivity in subtropical China, and explore the possible mechanisms underlying this relationship. My main assumption was that trees, at individual or stand level, growing in mixtures would produce higher biomass by an increase in leaf fraction as leaves are the light-acquiring organs and light competition is a major driver of forest dynamics. My study includes two methodological approaches: a large-scale experiment of artificially assembled tree communities, and a comparative study in secondary mixed broad-leaved forest stands. In both approaches I found that wood production increased with species richness, but I did not detect an effect of species richness on leaf production.

Using data of four annual inventories from when the tree diversity experiment was established, I observed the gradual emergence of a species richness effect on stand productivity (Chapter 1). At individual level, I observed that diversity enhanced stem growth but had no effect on leaf production (Chapter 2). In the comparative study, I found that more diverse stands had a higher stand basal area and aboveground biomass than less diverse stands. Furthermore, stands of high species diversity were characterized by higher variability in tree heights, which implies a more complex vertical structure. However, stand leaf area was similar among all stands (Chapter 3).

Biodiversity and ecosystem functioning (BEF) in forests

Over the last two decades, research on biodiversity-ecosystem functioning (BEF) has focused primarily on grasslands (Balvanera *et al.*, 2006). However, because of their importance in carbon sequestration at global scale, forests are receiving increasing attention, and are now considered the new frontier in biodiversity-ecosystem research (Mooney, 2005).

Observational and experimental studies have shown that aboveground productivity increases with tree richness across the globe (Vilà *et al.*, 2007; Paquette & Messier, 2011; Gamfeldt *et al.*, 2013; Baruffol *et al.*, 2013; Potvin & Gotelli, 2008). My results, both for the experimental and comparative study, do not only support this global trend but extend our knowledge about species diversity and ecosystem functioning in forests.

Firstly, this thesis broadens the geographical scope of BEF-research. Over the past 15 years tree diversity experiments in tropical to boreal biomes have been established, and are currently integrated in the largest network of biodiversity experiments worldwide, TreeDivNet (Verheyen *et al.*, 2015). Within the 18 tree experiments of TreeDivNet, 11 studies are located in temperate regions, with BEF-China the only experiment in the subtropics. Similarly, most observational studies have been carried out in temperate and boreal regions (Paquette & Messier, 2011; Gamfeldt *et al.*, 2013; see Nadrowski *et al.*, 2010, for a review). Thus, subtropical and tropical regions are still underrepresented in

BEF research in natural or semi-natural forests (but see Baruffol *et al.*, 2013; Lasky *et al.*, 2014; Poorter *et al.*, 2015).

By comparing BEF relationships in temperate and boreal forests Paquette & Messier (2011) hypothesized that diversity effects would be stronger in harsh environments, where facilitative interactions may be more important that competitive interactions. In addition, the role of niche and neutral processes in subtropical forest communities is still an ongoing question. As an example, the increase of richness along secondary succession in the BEF-China comparative plots is via random species immigration (Bruelheide *et al.*, 2011). In contrast, in the 24-ha permanent forest plot in the proximity of the BEF-China comparative plots, neutral processes and environmental controls can be equally important in shaping forest diversity (Legendre *et al.*, 2009) but their relative importance might depend on the spatial scale (Cheng *et al.*, 2012). If species are ecologically interchangeable, biodiversity effects on ecosystem functioning would be weak. Our results confirm that even in rich-species regions and complex ecosystems, diversity is an important driver of aboveground productivity. Similarly, in a recent large-scale observational study in highly diverse forests in the Neotropics, diversity enhanced aboveground biomass (Poorter *et al.*, 2015).

Furthermore, in both the young experimental stands and the mature successional stands of my comparative study, I observed a linear relationship between diversity and productivity. Thus, my results suggest that species richness is not redundant. This is in contrast to results of studies in the tropics, where mixtures were more productive than monocultures but species richness had no effect within mixtures of different species diversity (Potvin & Gotelli, 2008). Our result is even more outstanding if we consider that in the BEF-China experiment communities were randomly assembled from a 16-species pool following a 'broken stick' design. In other experiments that found an increase of stand basal area with tree richness in the Neotropics (Potvin & Gotelli, 2008; Ewel *et al.*, 2015), communities were built by choosing species that either differ in their growth rates (Potvin & Gotelli, 2008) or in the crown architecture and phenology (Ewel *et al.*, 2015), which could maximize the diversity effects. Thus, the BEF-China experiment may be more conservative than other studies.

Mechanisms underlying the BEF relationship in forests

To shed light on the mechanisms underlying the effect of tree species richness on aboveground productivity, the BEF-China experiment and comparative study allowed me to explore several paths.

Since initial population sizes and recruitment (through replanting) are controlled in the tree experiment, I could test which component of stand growth, i.e. gain of biomass due to growth of surviving trees, gain of biomass due to recruitment, and loss of biomass due to mortality, drove of the BEF relationship in young experimental stands. I found that more diverse plots had a higher stand basal area due to the increased growth of surviving trees (survival growth). Similarly, Lasky *et al.* (2014) found that in early successional stands (age 10–23 years) in a Neotropical forest, survival growth increases with tree species

richness. However, I suggest that mortality will become more important in determining stand dynamics and shaping the biodiversity-productivity relationship in the next years. Although for this study, neither tree density nor mortality rates were influenced by tree richness, I predict that intraspecific competition will further increase in monocultures and self-thinning will occur. As an example, in a Neotropic experimental study, tree density was similar between mixtures and monocultures for the first 5 years, but after which density in monocultures decreased (Ewel *et al.*, 2015).

In contrast, it is more difficult to assess the role of recruitment and mortality in the comparative plots. Whereas tree density did not influence stand growth of canopy trees (Chapter 3 and Baruffol *et al.*, 2013), it did enhance stand growth of understory trees (Baruffol *et al.*, 2013). Given the short time span of both studies (2–4 years) only few trees died or were recruited, and we did not assess biomass changes due to mortality or recruitment. A long-term study to monitor both demographic processes would allow us to test whether there is an effect on such processes of tree species richness, and whether their importance depends of successional age. In a Neotropical forest, biomass loss due to tree mortality is higher in more diverse stands but only in mid-sucessional stands (Lasky *et al.*, 2014).

But what are the exact mechanisms explaining higher stand basal area growth in more diverse stands? In mature forest the complementary use of the canopy has been proposed as the main mechanism for higher stand productivity. Similarly, in young successional forest stands increments of stand biomass are correlated with phylogenetic and leaf trait functional diversity (Lasky *et al.*, 2014), which further suggests the importance of the leaf fraction in explaining the BEF effect. Thus, in both the experimental and comparative study, I tested the effect of tree species richness on leaf production.

In my experimental study, I followed a detailed methodology at individual level. I visually estimated the numbers of leaves in each tree, and followed the fate of leaf cohorts to assess leaf emergence and mortality rates. Although individual stem growth increased with species richness, I did not detect such an effect on leaf production. In my comparative study, more diverse stands showed larger wood production and vertical structure, suggesting a more efficient use of the canopy space through a multi-layered canopy. However, stand leaf area was similar for all stands. Thus, my results suggest that BEF relationships, either in young or in old stands, are not mediated by an increase in leaf production.

We can not, however, discard light partitioning as a mechanism underlying the BEF relationship. Even if leaf production is similar for all stands, light absorption and use efficiency could vary because of morphological, physiological and structural factors, such as leaf morphology (Poorter *et al.*, 2012), inter- and intraspecific differences in net assimilation rates (Li, 2011), or clumping of trees that leads to shading among crowns (Binkley *et al.*, 2013). Processes other than photosynthesis may, however, control plant growth, e.g. nitrogen availability (Norby *et al.*, 2010; Norby & Zak, 2011; Palacio *et al.*, 2014; Körner, 2015). Indeed, a 10-year old biodiversity experiment recently showed that litter-mediated interactions among trees contribute more to overyielding than light partitioning (Sapijanskas *et al.*, 2013).

Perspectives and future research

In this thesis I have demonstrated that tree species richness increases aboveground productivity, both in young experimental stands and in older secondary successional stands. My results do not support the hypothesis that the complementarity use of the canopy leads to an increase in leaf production. However, I do not reject the possibility that the mechanism driving the BEF relationship may be light partitioning. Rather, I suggest the study of physiological and architectural traits that may influence light capture and use efficiency. Currently, other subprojects of the BEF-China consortium are studying functional traits and tree architecture. A comprehensive analysis will be crucial to understand complex systems, as forests.

Furthermore, in the BEF-China experiment diversity loss was simulated following a random extinction scenario, and two ecologically realistic non-random extinction scenarios (based on leaf traits and local species abundance). In this thesis, I used data from the random extinction scenario. In a preliminary analysis (of all scenarios), I observed that the type of extinction scenario has an effect on stand productivity. The analysis of such scenarios will shed light on the role of functional traits and increase our understanding of the real effect of diversity loss .

The BEF-China experiment includes monocultures of two timber species, *Pinus massoniana* and *Cunninghamia lanceolata*. These plots are of importance as a reference value for forestry managers. As plantations in China play a major role in carbon sequestration, the BEF-China experiment will identify productive species driving the BEF relationship (e.g. *C. axillaris* and *S. superba*) and assess their performance in comparison to timber species.

Conclusion

Using a experimental and comparative study approach, I demonstrated that tree diversity enhances aboveground productivity in subtropical China. Thus, diversity should not be only a conservation goal but a management strategy.

Although the longevity of trees and their slow growth (in comparison to grasslands) is often seen as a disadvantage for the establishment of tree experiments, the first results of the BEF-China experiment are encouraging. Indeed, the 'slow-motion' of tree interactions allows us to study subtle changes at stand and individual level.

Acknowledgments

I first would like to thank Pascal A. Niklaus for his supervision and support. Thank you for your guidance on statistics and R, and for allowing me to work independently in my project. Second, I would like to thank Bernhard Schmid for letting me be part of the BEF-China project, his enthusiasm for science and his decisive support in the last phase of my PhD.

My gratitude goes to Prof. Keping Ma and his group in Beijing for their scientific input and support. A special thanks to Xiaojuan Liu and Yang Bo for their amazing organizational skills, optimism, and immense patience to answer all my questions. I would also like to acknowledge Zhen Kai for his support in the field.

I would like to thank Prof. Yu Mingjian for sharing his knowledge about forest ecology. I really appreciated our email communications.

I extend a debt of gratitude to the SP1 students, Martin Baruffol, Xiulian Chi, David Emmerth and Yuanyuan Huang, for sharing their field data with me. You are the best example of hard work and generosity.

I am grateful to the BEF-China consortium for their administrative and technical support, especially to Sabine Both, Karin Nadrowski and Gunnar Seidler for helping me with the 'mysterious' plots in the project database and the replanting data.

I am also indebted to the students and farmers who helped me in the field. Particularly, I would like to thank Wei Xin, Ming Kuan, Mr. Jiang and Mr. Qi for their enthusiasm and dedication. It was a pleasure to work and share time with you.

My field work in China would have not been possible without the help of other members and students of the BEF-China project. A special thanks to Chen Lin for her logistic support (and teaching me how to harvest bamboo shoots); to Ying Li for working together in the inventories of the Main Experiment; to Christoph Hahn for helping me with my hemispheric pictures in Gutianshan (and sharing the boredom of Gutianshan in spring); to David Emmerth for teaching me how to assess leaf demography (and how to order baozi and noodle soup for breakfast); to Xiulian Chi and Yuanyuan Huang for their guidance in Gutianshan and encouraging words; and to Juliet Blum for her support and for our excursions to Wuyuan and Shanghai. You made my life in China a great and memorable experience.

I am also grateful to my IEU colleagues. Thank you to the post-docs, Mollie Brooks, Dan Flynn, Mikey O'Brien and Cam Wagg, for their scientific advice and reading my drafts. Thank you to Debra Zuppinger-Dingley, Inge Juszak, Janielle Porter and Sofia van Moorsel for your immense help in the final stretch of my thesis writing. I really appreciate the time you took to read my chapters, translate my abstract to German and help me with LaTeX. Thank you to Juliana Nates for helping me with my data and to Matteo Brezzi for solving my random questions about R, stats and China. I would also like to thank the administrative and technical staff, particularly Isabel Schöchli, Lilian

Dutoit, Jacqueline Moser, and Michel Nakano, for keeping paper work under control and keeping my computers safe and clean. I am also thankful to my fellow PhD students for their company, friendship and emotional support.

I would like to thank my friends in Lima and Zurich for always being there for a coffee, a beer or a phone call. You have kept me sane. I am also thankful to my parents, my siblings and my extended family in Lima for their love and moral support. *Gracias por estar siempre ahí, apoyándome en cada paso y decisión.* And last, thank you to Patrick, for his immense help in the field, his endless love and encouragement throughout this entire journey. *Merci pour toutes les aventures passées ensemble, celles d'alors, d'aujourd'hui et de demain.*

Curriculum vitae

Surname: Castro Izaguirre
First name: Nadia Cristina
Date of birth: 28 September 1978
Nationality: Peru

Education

2011 – 2016 Ph.D. Life Science Graduate Program Ecology Department of Evolutionary Biology and Environmental Studies

University of Zurich, Switzerland

Thesis: Aboveground primary productivity in forest ecosystems as a function of species diversity and composition.

2006 – 2009 MSc in Biodiversity and Ecology University Georg-August Göttingen, Germany

Thesis: Post-dispersal seed fate in primary and secondary forests in a Peruvian rainforest.

1998-2005 BS in Biology La Molina National Agrarian University, Peru

Thesis: Temporal Variation of Breeding Success of the Humboldt penguin at Punta San Juan, Peru (2000–2003).

1997 Abitur Deutsche Schule Alexander von Humboldt, Peru

Conference contributions

N. Castro, X. Chi, Z. Tang, M. Baruffol, B. Schmid and P.A. Niklaus Tree diversity enhances stand productivity but has no effect on leaf area index in subtropical forest, *45th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland*, Göttingen, 2015 (talk)

N. Castro and P.A. Niklaus Tree diversity enhances stand productivity in a large-scale field experiment in subtropical China, *99th ESA Annual Meeting*, Sacramento, 2014 (talk)

Bibliography

Alroy, J. (2015) Current extinction rates of reptiles and amphibians. *Proceedings of the National Academy of Sciences* **112**, 13003–13008.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology letters* **9**, 1146–1156.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011) Has the earth's sixth mass extinction already arrived? *Nature* **471**, 51–57.

Baruffol, M., Schmid, B., Bruelheide, H., Chi, X., Hector, A., Ma, K., Michalski, S., Tang, Z. & Niklaus, P.A. (2013) Biodiversity promotes tree growth during succession in subtropical forest. *PLoS ONE* **8**, e81246.

Bell, T., Lilley, A.K., Hector, A., Schmid, B., King, L. & Newman, J.A. (2009) A linear model method for biodiversity-ecosystem functioning experiments. *The American Naturalist* **174**, 836–849.

Binkley, D. (2003) Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. *Canadian Journal of Forest Research* **33**, 2274–2279.

Binkley, D., Campoe, O.C., Gspaltl, M. & Forrester, D.I. (2013) Light absorption and use efficiency in forests: Why patterns differ for trees and stands. *Forest Ecology and Management* **288**, 5 – 13.

Binkley, D., Senock, R., Bird, S. & Cole, T.G. (2003) Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and nitrogen-fixing *Facaltaria moluccana*. *Forest Ecology and Management* **182**, 93 – 102.

Binkley, D., Stape, J.L., Bauerle, W.L. & Ryan, M.G. (2010) Explaining growth of individual trees: Light interception and efficiency of light use by *Eucalyptus* at four sites in Brazil. *Forest Ecology and Management* **259**, 1704 – 1713.

Böhnke, M. & Bruelheide, H. (2013) How do evergreen and deciduous species respond to shade? — tolerance and plasticity of subtropical tree and shrub species of South-East China. *Environmental and Experimental Botany* **87**, 179 – 190.

Böhnke, M., Kreißig, N., Kröber, W., Fang, T. & Bruelheide, H. (2012) Wood trait-environment relationships in a secondary forest succession in South-East China. *Trees* **26**, 641–651.

Brassard, B.W., Chen, H.Y.H., Bergeron, Y. & Paré, D. (2011) Differences in fine root productivity between mixed- and single-species stands. *Functional Ecology* **25**, 238–246.

Bruelheide, H., Böhnke, M., Both, S., Fang, T., Assmann, T., Baruffol, M., Bauhus, J., Buscot, F., Chen, X.Y., Ding, B.Y. *et al.* (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* **81**, 25–41.

Bruelheide, H., Nadrowski, K., Assmann, T., Bauhus, J., Both, S., Buscot, F., Chen, X.Y., Ding, B., Durka, W., Erfmeier, A., Gutknecht, J.L.M., Guo, D., Guo, L.D., Härdtle, W., He, J.S., Klein, A.M., Kühn, P., Liang, Y., Liu, X., Michalski, S., Niklaus, P.A., Pei, K., Scherer-Lorenzen, M., Scholten, T., Schuldt, A., Seidler, G., Trogisch, S., von Oheimb, G., Welk, E., Wirth, C., Wubet, T., Yang, X., Yu, M., Zhang, S., Zhou, H., Fischer, M., Ma, K. & Schmid, B. (2014) Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. *Methods in Ecology and Evolution* **5**, 74–89.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M. & Weis, J.J. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences* **104**, 18123–18128.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.

Chen, H.Y., Klinka, K. & Kayahara, G.J. (1996) Effects of light on growth, crown architecture, and specific leaf area for naturally established *Pinuscontorta* var. *latifolia* and *Pseudotsugamenziesii* var.*glauca* saplings. *Canadian Journal of Forest Research* **26**, 1149–1157.

Cheng, J., Mi, X., Nadrowski, K., Ren, H., Zhang, J. & Ma, K. (2012) Separating the effect of mechanisms shaping species-abundance distributions at multiple scales in a subtropical forest. *Oikos* **121**, 236–244.

Cheng, X., Umeki, K., Honjo, T. & Mizusaki, D. (2014) Basal area growth rates of five major species in a *Pinus-Cunninghamia* forest in eastern China affected by asymmetric competition and spatial autocorrelation. *Journal of Forest Research* **19**, 86–96.

Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebber, D.P., Bin, Y., Bohlman, S.A., Bourg, N.A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., CÃ¡rdenas, D., Chang, L.W., Chiang, J.M., Chuyong, G., Condit, R., Dattaraja, H.S., Davies, S., Duque, A., Fletcher, C., Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R.D., Howe, R., Hsieh, C.F., Hubbell, S.P., Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson, A.J., Lian, J., Lin, D., Liu, H., Lutz, J.A., Ma, K., Malhi, Y., McMahon, S., McShea, W., Meegaskumbura, M., Mohd. Razman, S., Morecroft, M.D., Nytch, C.J., Oliveira, A., Parker, G.G., Pulla, S., Punchi-Manage, R., Romero-Saltos, H., Sang, W., Schurman, J., Su, S.H., Sukumar, R., Sun, I.F., Suresh, H.S., Tan, S., Thomas, D., Thomas, S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z. & Zimmerman, J.K. (2013) Scale-dependent relationships between tree species richness and ecosystem function in forests. *Journal of Ecology* **101**, 1214–1224.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R. & Ni, J. (2001) Measuring net primary production in forests: concepts and field methods. *Ecological applications* **11**, 356–370.

Dirzo, R. & Raven, P.H. (2003) Global state of biodiversity and loss. *Annual Review of Environment and Resources* **28**, 137–167.

Editorial Committee for Flora Reipublicae Popularis Sinicae (2004) *Flora Reipublicae Popularis Sinicae*. Science Press, Beijing.

eFloras (2008) Flora of china. `http://www.efloras.org`, accessed 19 November 2015.

Egli, P. & Schmid, B. (2001) The analysis of complex leaf survival data. *Basic and Applied Ecology* **2**, 223–231.

Ewel, J.J., Celis, G. & Schreeg, L. (2015) Steeply increasing growth differential between mixture and monocultures of tropical trees. *Biotropica* **47**, 162–171.

Falster, D.S. & Westoby, M. (2003) Leaf size and angle vary widely across species: what consequences for light interception? *New Phytologist* **158**, 509–525.

Fang, J., Chen, A., Peng, C., Zhao, S. & Ci, L. (2001) Changes in forest biomass carbon storage in China between 1949 and 1998. *Science* **292**, 2320–2322.

FAO (2010) *Global Forest Resources Assessment 2010: Main Report*. FAO forestry paper, Food and Agriculture Organization of the United Nations, Rome, Italy.

Fargione, J., Tilman, D., Dybzinski, R., Lambers, J.H.R., Clark, C., Harpole, W.S., Knops, J.M., Reich, P.B. & Loreau, M. (2007) From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society B: Biological Sciences* **274**, 871–876.

Fox, J.W. (2005) Interpreting the 'selection effect' of biodiversity on ecosystem function. *Ecology Letters* **8**, 846–856.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D. *et al.* (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature communications* **4**, 1340.

Givnish, T.J. (2010) On the adaptive significance of compound leaves, with particular reference to tropical trees. *Tropical trees as living systems* (eds. P.B. Tomlinson & M. Zimmerman), p. 351, Cambridge University Press.

Guariguata, M.R. & Ostertag, R. (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* **148**, 185 – 206.

Guchou, S., Xiaoping, Z., Xiaojing, L. & Ping, Z. (2007) Effects of moderate high-temperature stress on photosynthesis in three saplings of the constructive tree species of subtropical forest. *Acta Ecologica Sinica* **27**, 1283 – 1290.

Guisasola, R., Tang, X., Bauhus, J. & Forrester, D.I. (2015) Intra- and inter-specific differences in crown architecture in Chinese subtropical mixed-species forests. *Forest Ecology and Management* **353**, 164 – 172.

Hardiman, B., Bohrer, G., Gough, C., Vogel, C. & Curtis, P. (2011) The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. *Ecology* **92**, 1818–1827.

Hardiman, B., Gough, C., Halperin, A., Hofmeister, K., Nave, L., Bohrer, G. & Curtis, P. (2013) Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function. *Forest Ecology and Management* **298**, 111 – 119.

Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* **89**, 947–959.

Harper, J.L. *et al.* (1977) Population biology of plants. *Population biology of plants.* .

Healy, C., Gotelli, N.J. & Potvin, C. (2008) Partitioning the effects of biodiversity and environmental heterogeneity for productivity and mortality in a tropical tree plantation. *Journal of Ecology* **96**, 903–913.

Hector, A. (2009) Darwin's 'principle of divergence' and the link between biodiversity and ecosystem functioning. *Darwin und die Botanik* (ed. E. Stöcklin J; Höxtermann), pp. 182–191, Basilisken-Presse, Ransdorf.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M., Diemer, M., Dimitrakopoulos, P., Finn, J., Freitas, H., Giller, P., Good, J. *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–1127.

Hooper, D., Chapin Iii, F., Ewel, J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J., Lodge, D., Loreau, M., Naeem, S. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs* **75**, 3–35.

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography (MPB-32)*, vol. 32. Princeton University Press.

Jacob, M., Leuschner, C. & Thomas, F.M. (2010) Productivity of temperate broad-leaved forest stands differing in tree species diversity. *Annals of Forest Science* **67**, 503.

Jucker, T., Bouriaud, O., Avacaritei, D. & Coomes, D.A. (2014a) Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecology Letters* **17**, 1560–1569.

Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F. & Coomes, D.A. (2014b) Competition for light and water play contrasting roles in driving diversity - productivity relationships in Iberian forests. *Journal of Ecology* **102**, 1202–1213.

Jucker, T., Bouriaud, O. & Coomes, D.A. (2015) Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Functional Ecology* **29**, 1078–1086.

Klinka, K., Wang, Q., Kayahara, G.J., Carter, R.E. & Blackwell, B.A. (1992) Light-growth response relationships in Pacific silver fir (*Abies amabilis*) and subalpine fir (*Abies lasiocarpd*). *Canadian Journal of Botany* **70**, 1919–1930.

Körner, C. (2015) Paradigm shift in plant growth control. *Current Opinion in Plant Biology* **25**, 107 – 114.

Kröber, W., Böhnke, M., Welk, E., Wirth, C. & Bruelheide, H. (2012) Leaf trait-environment relationships in a subtropical broadleaved forest in south-east China. *PLoS ONE* **7**, e35742.

Lang, A.C., Härdtle, W., Bruelheide, H., Geißler, C., Nadrowski, K., Schuldt, A., Yu, M. & von Oheimb, G. (2010) Tree morphology responds to neighbourhood competition and slope in species-rich forests of subtropical China. *Forest Ecology and Management* **260**, 1708 – 1715.

Lasky, J.R., Uriarte, M., Boukili, V.K., Erickson, D.L., John Kress, W. & Chazdon, R.L. (2014) The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecology Letters* **17**, 1158–1167.

Lebourgeois, F., Gomez, N., Pinto, P. & Mérian, P. (2013) Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *Forest Ecology and Management* **303**, 61 – 71.

Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I.F. & He, F. (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* **90**, 663–674.

Li, X. (2011) *Light-use strategies and biomass accumulation of woody species in a subtropical forest in southwest China*. Phd thesis, University of Zurich, Zurich, Switzerland.

Li, Y., Härdtle, W., Bruelheide, H., Nadrowski, K., Scholten, T., von Wehrden, H. & von Oheimb, G. (2014) Site and neighborhood effects on growth of tree saplings in subtropical plantations (China). *Forest Ecology and Management* **327**, 118 – 127.

Liang, J., Buongiorno, J., Monserud, R.A., Kruger, E.L. & Zhou, M. (2007) Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. *Forest Ecology and Management* **243**, 116 – 127.

Lin, D., Lai, J., Muller-Landau, H.C., Mi, X. & Ma, K. (2012) Topographic variation in aboveground biomass in a subtropical evergreen broad-leaved forest in China. *PLoS ONE* **7**, e48244.

Lohbeck, M., Poorter, L., Martínez-Ramos, M., Rodriguez-Velázquez, J., van Breugel, M. & Bongers, F. (2014) Changing drivers of species dominance during tropical forest succession. *Functional Ecology* **28**, 1052–1058.

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* **294**, 804–808.

Marquard, E., Weigelt, A., Temperton, V.M., Roscher, C., Schumacher, J., Buchmann, N., Fischer, M., Weisser, W.W. & Schmid, B. (2009) Plant species richness and functional composition drive overyielding in a six-year grassland experiment. *Ecology* **90**, 3290–3302.

McElhinny, C., Gibbons, P., Brack, C. & Bauhus, J. (2005) Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management* **218**, 1 – 24.

Meinen, C., Hertel, D. & Leuschner, C. (2009) Root growth and recovery in temperate broad-leaved forest stands differing in tree species diversity. *Ecosystems* **12**, 1103–1116.

Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being*, vol. 5. Island Press Washington, DC.

Mokany, K., Raison, R. & Prokushkin, A. (2006) Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change Biology* **12**, 84–96.

Mooney, H. (2005) Foreword. *Forest Diversity and Function*, pp. 87–108, Springer.

Morin, X., Fahse, L., Scherer-Lorenzen, M. & Bugmann, H. (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters* **14**, 1211–1219.

Nadrowski, K., Wirth, C. & Scherer-Lorenzen, M. (2010) Is forest diversity driving ecosystem function and service? *Current Opinion in Environmental Sustainability* **2**, 75–79.

Naeem, S., Duffy, J.E. & Zavaleta, E. (2012) The functions of biological diversity in an age of extinction. *Science* **336**, 1401–1406.

Niinemets, Ü. (2010) A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecological Research* **25**, 693–714.

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E. & McMurtrie, R.E. (2010) CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences* **107**, 19368–19373.

Norby, R.J. & Zak, D.R. (2011) Ecological lessons from free-air CO_2 enrichment (FACE) experiments. *Annual Review of Ecology, Evolution, and Systematics* **42**, 181–203.

Pacala, S.W., Canham, C.D., Jr., J.A.S. & Kobe, R.K. (1994) Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* **24**, 2172–2183.

Pakkad, G., Torre, F., Elliott, S. & Blakesley, D. (2003) Selecting seed trees for a forest restoration program: a case study using *Spondias axillaris* roxb. (Anacardiaceae). *Forest Ecology and Management* **182**, 363 – 370.

Palacio, S., Hoch, G., Sala, A., Körner, C. & Millard, P. (2014) Does carbon storage limit tree growth? *New Phytologist* **201**, 1096–1100.

Pan, Y., Birdsey, R.A., Phillips, O.L. & Jackson, R.B. (2013) The structure, distribution, and

biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics* **44**, 593–622.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* **20**, 170–180.

Parrotta, J.A. (1999) Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. *Forest Ecology and Management* **124**, 45 – 77.

Peng, S. (2014) *Effects of Plant Diversity on Leaf Area Index in Subtropical Forest in China*. Msc thesis, University of Zurich, Zurich, Switzerland.

Petchey, O.L. (2003) Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos* **101**, 323–330.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* **9**, 741–758.

Petriţan, A., von Lüpke, B. & Petriţan, I. (2009) Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings. *European Journal of Forest Research* **128**, 61–74.

Piotto, D. (2008) A meta-analysis comparing tree growth in monocultures and mixed plantations. *Forest Ecology and management* **255**, 781–786.

Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P. & Mommer, L. (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* **193**, 30–50.

Poorter, L. & Rozendaal, D. (2008) Leaf size and leaf display of thirty-eight tropical tree species. *Oecologia* **158**, 35–46.

Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., Álvarez Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., Carvalho, F.A., Casanoves, F., Cornejo-Tenorio, G., Costa, F.R.C., de Castilho, C.V., Duivenvoorden, J.F., Dutrieux, L.P., Enquist, B.J., Fernández-Méndez, F., Finegan, B., Gormley, L.H.L., Healey, J.R., Hoosbeek, M.R., Ibarra-Manríquez, G., Junqueira, A.B., Levis, C., Licona, J.C., Lisboa, L.S., Magnusson, W.E., Martínez-Ramos, M., Martínez-Yrizar, A., Martorano, L.G., Maskell, L.C., Mazzei, L., Meave, J.A., Mora, F., Muñoz, R., Nytch, C., Pansonato, M.P., Parr, T.W., Paz, H., Pérez-García, E.A., Rentería, L.Y., Rodríguez-Velazquez, J., Rozendaal, D.M.A., Ruschel, A.R., Sakschewski, B., Salgado-Negret, B., Schietti, J., Simões, M., Sinclair, F.L., Souza, P.F., Souza, F.C., Stropp, J., ter Steege, H., Swenson, N.G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N. & Peña Claros, M. (2015) Diversity enhances carbon storage in tropical forests. *Global Ecology and Biogeography* **24**, 1314–1328.

Potvin, C. & Gotelli, N.J. (2008) Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecology Letters* **11**, 217–223.

Purves, D. & Pacala, S. (2008) Predictive models of forest dynamics. *Science* **320**, 1452–1453.

Purves, D.W., Lichstein, J.W., Strigul, N. & Pacala, S.W. (2008) Predicting and understanding forest dynamics using a simple tractable model. *Proceedings of the National Academy of Sciences* **105**, 17018–17022.

R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P., Uhl, C., Walters, M., Prugh, L. & Ellsworth, D.S. (2004) Leaf demography and phenology in Amazonian rain forest: a census of 40 000 leaves of 23 tree species. *Ecological Monographs* **74**, 3–23.

Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B. & Eisenhauer, N. (2012) Impacts of biodiversity loss escalate through time as redundancy fades. *Science* **336**, 589–592.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P. & Foley, J.A. (2009) A safe operating space for humanity. *Nature* **461**, 472–475.

Roscher, C., Schumacher, J., Weisser, W.W., Schmid, B. & Schulze, E.D. (2007) Detecting the role of individual species for overyielding in experimental grassland communities composed of potentially dominant species. *Oecologia* **154**, 535–549.

Roscher, C., Temperton, V.M., Scherer-Lorenzen, M., Schmitz, M., Schumacher, J., Schmid, B., Buchmann, N., Weisser, W.W. & Schulze, E.D. (2005) Overyielding in experimental grassland communities - irrespective of species pool or spatial scale. *Ecology Letters* **8**, 419–429.

Rozendaal, D.M.A., Hurtado, V.H. & Poorter, L. (2006) Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology* **20**, 207–216.

Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J. & Zavala, M.A. (2014) Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography* **23**, 311–322.

Russo, S.E., Davies, S.J., King, D.A. & Tan, S. (2005) Soil-related performance variation and distributions of tree species in a Bornean rain forest. *Journal of Ecology* **93**, 879–889.

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N. & Loreau, M. (2014) Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology* **95**, 2479–2492.

Sapijanskas, J., Potvin, C. & Loreau, M. (2013) Beyond shading: Litter production by neighbors contributes to overyielding in tropical trees. *Ecology* **94**, 941–952.

Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Schmid, B., Hector, A., Bornik, Z., Reynolds, G. & Schulze, E.D. (2005) The design of experimental tree plantations for functional biodiversity research. *Forest Diversity and Function*, pp. 347–376, Springer.

Schleppi, P., Conedera, M., Sedivy, I. & Thimonier, A. (2007) Correcting non-linearity and slope effects in the estimation of the leaf area index of forests from hemispherical photographs. *Agricultural and Forest Meteorology* **144**, 236 – 242.

Seidel, D., Leuschner, C., Scherber, C., Beyer, F., Wommelsdorf, T., Cashman, M.J. & Fehrmann, L. (2013) The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest. *Forest Ecology and Management* **310**, 366 – 374.

Selaya, N., Oomen, R., Netten, J., Werger, M. & Anten, N. (2008) Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession. *Journal of Ecology* **96**, 1211–1221.

Shen, Y., Santiago, L., Shen, H., Ma, L., Lian, J., Cao, H., Lu, H. & Ye, W. (2014) Determinants of change in subtropical tree diameter growth with ontogenetic stage. *Oecologia* **175**, 1315–1324.

Shi, L., Zhao, S., Tang, Z. & Fang, J. (2011) The changes in China's forests: An analysis using the forest identity. *PLoS ONE* **6**, e20778.

Srivastava, D.S., Cadotte, M.W., MacDonald, A.A.M., Marushia, R.G. & Mirotchnick, N. (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters* **15**, 637–648.

Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., de Vries, W., de Wit, C.A., Folke, C., Gerten, D., Heinke, J., Mace, G.M., Persson, L.M., Ramanathan, V., Reyers, B. & Sörlin, S. (2015) Planetary boundaries: Guiding human development on a changing planet. *Science* **347**.

Thimonier, A., Sedivy, I. & Schleppi, P. (2010) Estimating leaf area index in different types of mature forest stands in Switzerland: a comparison of methods. *European Journal of Forest Research* **129**, 543–562.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science* **294**, 843–845.

Verheyen, K., Vanhellemont, M., Auge, H., Baeten, L., Baraloto, C., Barsoum, N., Bilodeau-Gauthier, S., Bruelheide, H., Castagneyrol, B., Godbold, D., Haase, J., Hector, A., Jactel, H., Koricheva, J., Loreau, M., Mereu, S., Messier, C., Muys, B., Nolet, P., Paquette, A., Parker, J., Perring, M., Ponette, Q., Potvin, C., Reich, P., Smith, A., Weih, M. & Scherer-Lorenzen, M. (2015) Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio* pp. 1–13.

Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase, J., Kunstler, G., Schelhaas, M. & Trasobares, A. (2013) Disentangling biodiversity and climatic determinants of wood production. *PLoS ONE* **8**, e53530.

Vilà, M., Vayreda, J., Comas, L., Ibáñez, J.J., Mata, T. & Obón, B. (2007) Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters* **10**, 241–250.

Wang, L., Li, L., Chen, X., Tian, X., Wang, X. & Luo, G. (2014) Biomass allocation patterns across China's terrestrial biomes. *PLoS ONE* **9**, e93566.

Wang, X.H., Kent, M. & Fang, X.F. (2007) Evergreen broad-leaved forest in Eastern China: its ecology and conservation and the importance of resprouting in forest restoration. *Forest Ecology and Management* **245**, 76–87.

Xiang, W., Liu, S., Lei, X., Frank, S., Tian, D., Wang, G. & Deng, X. (2013) Secondary forest floristic composition, structure, and spatial pattern in subtropical China. *Journal of Forest Research* **18**, 111–120.

Xu, B., Guo, Z., Piao, S. & Fang, J. (2010) Biomass carbon stocks in China's forests between 2000 and 2050: A prediction based on forest biomass-age relationships. *Science China Life Sciences* **53**, 776–783.

Yang, X., Bauhus, J., Both, S., Fang, T., Härdtle, W., Kröber, W., Ma, K., Nadrowski, K., Pei, K., Scherer-Lorenzen, M. *et al.* (2013) Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). *European Journal of Forest Research* **132**, 593–606.

Young, B., Liang, J. & Chapin, III, F. (2011) Effects of species and tree size diversity on recruitment in the Alaskan boreal forest: A geospatial approach. *Forest Ecology and Management* **262**, 1608 – 1617.

Zhang, Y. & Chen, H.Y.H. (2015) Individual size inequality links forest diversity and aboveground biomass. *Journal of Ecology* **103**, 1245–1252.

Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology* **100**, 742–749.